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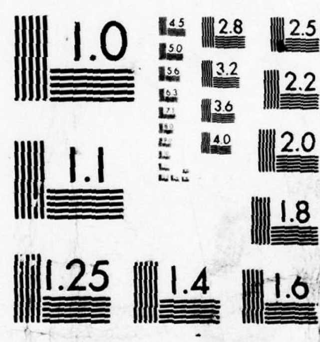

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Contents:

THE STRUCTURE AND FUNCTIONS OF CETACEAN SCHOOLS

by

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Introduction

We define a school as any aggregation of aquatic animals that regularly swim together as a unit. This definition is purposely broader than most that have been proposed (see Shaw, 1970, for a review). This breadth is necessary, we feel, because the functions of school formation are themselves the diverse, almost universally occurring needs of free-swimming aquatic animals. In the broadest view, the school provides for social animals the conditions for living in open water. Also, since schools change shape, size and constituent numbers under differing conditions, it is obvious that these conditions for living are expressed as equilibria between dispersive and attractive forces (see Breder, 1954).

The factors that affect the structure of cetacean schools are diverse and can be categorized in a variety of ways. We choose to subdivide them for convenience into a series of roughly separate functional categories. Such a categorization, while to a degree overlapping, will help us to perceive and understand variations in school structure.

It may be that the primary cause of cetacean schools centers around protection from predation, as is suggested by Williams' (1964) cover-seeking concept, or Hamilton's (1971) "selfish herd" model. Another view concerning the cause of schooling or flocking is that the schooling tendency is food-based, being a response to unpredictable patchy food. This has been shown to be the case for colonial nesting and flocking of Great Blue Herons, Ardea herodias (Krebs, 1974) and for wagtails, Motocilla sp. (Zahavi, 1971). Wagtail groups fluctuate from a territorial system when the food supply is predictable, to a flock when it is irregularly distributed. Whatever the cause, during the course of evolution a variety of other functions have developed or been transferred to the context of the school.

We perceive the following activities of open water social animals that either require schools or affect their structure.

1. Food Related Activity
2. Reproduction and Growth
3. Social Integration and Communication
4. Learning
5. Protective Behavior
6. Responses to Environmental Cycles

Most Dolphins spend their entire lives in moving schools. Being highly social advanced mammals one can expect their intra-school relationships to be complex, and in fact, expect that the school is the matrix within which the complexities of these animals are mostly to be understood. This does not imply, however, that the dolphin school is necessarily a permanent

unit of a given size, formed of the same individuals from day to day. In some species such as the spinner porpoise (Norris and Dohl, ms) it clearly is not, and instead school sizes may vary widely and individuals or small groups may move freely from small to large aggregations.

Cetaceans are exceptionally difficult forms to study and rather little rigorous study has been performed. Most data have come from fisheries observations, casual observations at sea, or from relatively unnatural captive schools. The data reported here are mostly anecdotal and very fragmentary. Let us examine the information for each of the above categories.

Food Related Activity

Dolphins and whales feed largely upon schooling prey of various sorts, and are themselves schooling animals. Between such predators and their prey, food finding and capture strategies are pitted against concealment, avoidance or satiation strategies. Brock and Riffenburgh (1960) point out that large prey schools tend to satiate predators with excess numbers, and to maximize the cost of finding new prey. On the other hand, schooled predators may optimize capture. Major (1976) has demonstrated that schooled predatory fish are more efficient at food capture than single animals. This is also true of some large terrestrial mammalian predators (Kruuk, 1977, Shaller, 1972) and almost certainly true of dolphins. In examining these systemic relationships for dolphins we will consider two kinds of information; intraschool

optimization of food location and capture by odontocetes, and patterns of school movement that may allow optimal utilization of limited renewable food resources.

Many dolphin and small whale species are known or thought to use special feeding strategies. It seems intuitively obvious that all odontocetes have such strategies and that they will usually vary from species to species, depending upon the particular congeries of adaptations possessed by a given form. Sperm whales and spinner dolphins are not likely to use the same strategies, given their widely divergent structures and behavior. The literature contains many passing and a few detailed references to feeding strategy, and many references exist showing that a number of cetacean migrations or seasonal movement patterns are based upon seasonally abundant food supplies (see for example, Sergeant, 1962, for the pothead _Globicephala melaena_, and Norris and Prescott, 1961 for the northeastern Pacific pilot whatle _Globicephala scammoni_, and Neave and Wright, 1968, for the harbor porpoise _Phocoena phocoena_). Information on feeding strategies can be categorized into the following topics: (a) food searching patterns, (b) food capture patterns, and (c) learned patterns.

Food Searching Patterns

Dolphin species such as the common dolphin, _Delphinus delphis_, the spotted dolphin, _Stenella attenuata_, the spinner dolphin, _Stenella longirostris_, and the striped dolphin, _Lagenorhynchus_ sp., which travel in schools numbering in the hundreds or even thousands of animals often gather in schools that are broader

than long relative to the direction of school movement. The assumption is that such a school shape allows the group of animals to scan a wide swath of sea for food or enemies, with the aggregate echolocation sounds of many animals. Thus, such a school, which may be several kilometers broad, could scan a path of ocean of that width, or a little more. Given a 5 km/hr school speed, and one km width, 5 square kms of sea could be scanned per hour, an enormously increased efficiency when compared to the capability of a single animal. Since the food of cetaceans in such schools is typically formed of schooling species (such as surface dwelling or scattering layer fishes and squids; see Fitch and Brownell, 1968, anchovies and sprats; Tsalkin, 1938), location of food sources could thus support large groups of dolphins.

The mode of travel of various species during food searching varies considerably. Some, like pilot whales, move deliberately in broad ranks (Norris and Prescott, 1961), while spinner or spotted dolphins may move more rapidly, engaging in spectacular aerial behavior along the way. The right whale dolphin (Lissodelphis sp.) may at times move very rapidly and spend much time in the air (Tomilin, 1967). Its extremely attenuate body may allow it to take three or four rapid propulsive strokes of its flukes while its anterior body is in the air, thus reducing drag. At any rate, this species may be seen leaping in dense ranks, travelling considerable distances over the surface with each leap.

The most clearly defined case of lateral spreading of schools during food searching is probably found in the pilot whales in which rather modest numbers of animals (usually 100 or less) travel as a rank essentially abreast, during food finding. The lateral breadth of such schools may cover 2 kilometers or more at times. Similar behavior is often seen in the smaller killer while (Orcinus orca) schools.

It is interesting that the shape of fleeing schools is similar to schools searching for food, though generally much more tightly packed.

Searching may rely upon sea bottom topography as a guidepost. The best documented case of this sort has been reported for the species Delphinus delphis and Stenella longirostris by Evans (1974). Delphinus schools off southern California and Baja California were found to congregate with considerable predictability over escarpments and seamounts which might be as much as 2000 meters below the surface (Figure 1). It is surmised that the porpoises may be able to "hear" such topography by passive listening even though it is too deep to reach by diving since Evans reports an increase in ambient sea noise in such areas. Increased density of scattering layer organisms exist over such sea bottom topography as compared to sea bottom with less relief, and the stomach contents of porpoises concerned showed them to be feeding on fishes and squids of the vertical migrant layers, as well as upon surface anchovies. Whether the echolocation systems of such animals could be used to discriminate topography at such distances is a moot point.

Similar association of large toothed whales such as the sperm and Baird's beaked whale (Physeter catodon and Berardius bairdi) with subsurface seamounts has been reported to us by whalers at the Richmond Whaling Station, California, and was used by them as a guide to capture. Also, it is thought that large baleen whales such as the finback (Balaenoptera physalus) and the blue whale (B. musculus) migrate in the general region of the continental slope (Mackintosh, 1946), though this has not been correlated with feeding strategy.

In addition, smaller odontocetes frequent these same areas and must feed there. Included are the common dolphins, Delphinus delphis, and members of the genera Lissodelphis, Grampus, and Stenella. Studies of otoliths and squid beaks from stomach contents (Fitch and Brownell, 1968) show feeding upon vertical migrant or mesopelagic forms, some of which require dives in excess of 200 meters depth. Even though many of these food organisms are small, individual capture rather than batch feeding is required.

Baleen whales generally do not form the tightly cohesive schools seen in odontocetes. They are much more often seen widely dispersed or alone, though occasional large assemblages of baleen whales are encountered on feeding, breeding or calving grounds (Tomilin, 1967; Norris, 1967). Considering their capability at long distance sound transmission (Payne and Webb, 1971), it may be that the widely spread baleen whales should be considered as highly dispersed schools, perhaps covering many miles of sea.

An interesting sidelight on food search patterns is what has been called "social parasitism" by Norris and Prescott (1961). This behavior consists of small groups of dolphins of various species associating themselves with other species that are presumed to have more efficient food-finding capability. A typical example is the very common association of bottlenose dolphins (Tursiops) with northeastern Pacific pilot whale schools. Often small groups (20 or less) of bottlenose dolphins swim at the ends of pilot whale food-searching ranks. Two observations by Norris and Prescott (1961) showed that this sort of association cannot be called casual. When the pilot whales sounded, the bottlenose dolphins normally sounded with them, but usually surfaced well before the whales, presumably because of lesser breath-holding capabilities. However, the position of the dolphins on the surface was predictive of the place where the whales ultimately surfaced. That is to say the dolphins at the surface seemed to travel over the whales beneath. The second observation was of a group of right whale dolphins swimming with a pilot whale school. Observations were made simultaneously from an aircraft circling above the schools and from a capture vessel harrying the whale school. The aircraft reported that the right whale dolphins followed each evasive maneuver of the whales, changing course as they did, even though they were swimming an estimated kilometer away. Presumably contact was maintained acoustically.

A striking association of a somewhat different sort is that between tropical oceanic dolphins (principally Stenella and

Delphinus) and yellowfin tuna. The fish typically follow behind the dolphins and are presumably benefited by the food-finding abilities of them (Green, Perrin and Petrich, 1971). Even when the dolphins are herded by power boats, the tuna generally remain with them and can be netted. This behavior forms the basis for much of the purse seine tuna industry, and will be discussed in greater detail under "Optimization of Energy Supplies" later in this paper.

Seasonal movements of many and perhaps most cetacean schools seem regulated by variable food resources. For instance, Clarke (1957) and Sergeant (1962) report seasonal migration by pilot whale schools to be regulated by seasonal abundance of squid and schooling fish. Wilke, Taniwaki, and Kuroda (1953) report such migrations for the Dall purpoise, Phocoenoides dalli, the north Pacific striped dolphin, Lagenorhynchus obliquidens and Lissodelphis borealis along the shores of Japan. Similar references for food-related migrations of many cetacean species may be found in such summary volumes as that compiled by Tomilin (1967).

While most cetaceans seem to move widely in relation to prey aggregations, often on a seasonal basis, some species have more restricted ranges and can be seen from day to day in certain regions. The latter group includes those living in rivers and lakes, such as the platanistid dolphin of the Amazon-Oronoco Basins, the boutu (Inia geoffrensis) (see Layne, 1958), or the susu (Platanista gangetica) of the Ganges-Brahmaputra Rivers (Pilleri, 1970), or the belukha (Delphinapterus leucas) that

sometimes swims long distances up rivers during the downstream migration of salmon smolts. All of these forms, however, exhibit seasonal or other movements. It seems that topography simply channels or restricts movements like those normally seen in the open sea. Only those dolphins associating with oceanic islands, or perhaps certain features of the shoreline such as river mouths or bays, seem wholly restricted to specific geographic locations in part of their range. Some populations of the spinner dolphin, for example, habitually retreat to atoll lagoons during the day, presumably to rest (Norris and Dohl, ms), and historic records suggest that this behavior has long continuity through time. Only these latter forms, therefore, fit the definition of refuging forms, as developed by Hamilton and Watt (1970), and may be expected to have developed feeding relations such as core areas, trampling zones, and feeding arenas. An example is the school of spinner dolphins that each morning enter Bigej pass into the lagoon at Kwajalein Atoll, Marshall Islands, and leave late in the day, presumably to feed offshore (personal observation of K. Norris). The problem of attempting to describe the more usual cetacean feeding patterns in Hamilton and Watt's less restrictive category of the "radial pack" (that is "a pack moving within a restricted area") lies in the almost universal lack of information about the total range of movement of any species. Do schools move in definable areas, or are they wholly opportunistic? It seems that the answer for oceanic forms lies somewhere between these two extremes. Along the California coast, for example,

one can roughly recognize an inshore group of species, a continental shelf margin group and a central Pacific group. There are, however, records of all classes in nearshore waters on occasion. For instance, the oceanic false killer whale, Pseudorca crassidens, strands occasionally on San Nicolas Island (Mitchell, 1965), which is located on the continental shelf, and has been seen in a large school off nearshore Santa Catalina Island (Norris and Prescott, 1961), and the continental slope dwelling Pacific right whale dolphin is seen occasionally within a few kilometers of the California coast. These occurrences indicate movements of a hundred and sixty or more kilometers inshore of normal areas of occurrence, but even so, the general faunal separations can still be recognized, and hence restriction of a very fluid sort to general region of the sea occurs.

Food Capture Patterns

Food capture by odontocetes has been described in a number of cases. The behavior of schools during food capture typically differs strikingly from the searching mode. We classify the capture patterns as (a) spread school formations, and (b) cooperative capture methods.

It seems typical of oceanic schooling genera, such as Stenella and Delphinus, that once concentrations of food are located the form of the dolphin school changes. The frontally moving school enters a spread phase in which members may separate many times as far from their neighbors as during searching, and

the entire school may become discoidal, or essentially shapeless instead of ranked (see Saayman, Bower and Tayler, 1972). Evans (1974), Norris and Dohl (ms), and Tsalkin (1938) describe feeding schools in oceanic dolphins such as Delphinus and Stenella. Both genera, when feeding, spread over large areas of sea, reducing school cohesion, and breaking into small subgroups. Single animals may sometimes occur within the boundaries of such a school. For some species, diving patterns change markedly during the change from searching to feeding. During feeding in the spinner dolphin, dives become longer in duration and may become regular. Even though spread over a wide area of sea, Stenella schools may still continue to dive more or less synchronously, except in very large schools. In large spinner dolphin schools, for instance, such synchrony is not perfect and sections of a school a mile or more in largest dimension may dive or reach the surface with some independence. Nevertheless, it is impressive in such cases that considerable segments of such schools, even though widely spread, may dive together. Thus some sort of signal system, probably acoustic, must be involved in diving synchrony. It may also be that diving synchrony is part of the strategy of food capture. Many animals attacking a prey school may have a greater percentage of success than an animal fishing alone. Such feeding strategies are known for a variety of animals such as cormorant flocks (Bartholomew, 1942), shearwaters (Shallenberger, 1973), pinnipeds (Roger Gentry, personal communication) and fish (Major, 1976).

Spread formation begins at dusk and persists in darkness in spinner schools (Norris and Dohl, ms) but occurs in daytime in common dolphin schools (Evans, 1974). Thus these dolphin school formations may not have the same basis as Radakov (1967) ascribes for prey fish schools which disperse at night. He speculates that darkness protects scattered fish because the visual sense will fail to locate most individuals. Radakov maintains that daytime schooling is protective because it mathematically reduces the likelihood of a predator locating prey; using much the same argument as that presented by Brock and Riffenburgh (1960). We assume that spread formation in dolphins is, instead, a response to the needs of food-getting, and that echolocation allows it to be used at night even on rather dispersed prey.

Belukhas are reported to enter river mouths and rivers regularly in search of salmon smolts and other fish migrating seaward. Sometimes the aggregations at sea may be very numerous. For example, Tomilin (1967) reports about 10,000 belukhas in the Straits of Novaya Zemlya in pursuit of schooling fish migrating there in autumn. Belukhas are extremely sensitive to tidal changes during such feeding movements (Fish and Vania, 1971).

Considerable observation has been performed on Black Sea common dolphin (*Delphinus delphis*) schools, and their schooling and feeding patterns are probably as well known as for any small cetacean (Tsalkin, 1938; Barabash-Nikiforov, 1940; Golenchenko, 1949). The dolphins reportedly concentrate over abundant food in essentially stationary spread schools of great extent, numbering, according to Tsalkin, as many as 250,000 - 300,000 individuals.

When food organisms become sparse or disperse, the large dolphin schools fragment or move away. Irregular migrations are made following the two major food species, anchovies and sprats, which have different thermal requirements and hence move to varying parts of the sea. Mating groups were also noted from the air, with groups of 6-8 males and a single female reported, though parenthetically one wonders how accurate sex determination can be when carried out from the air, even though they report seeing males with erections (Tomilin, 1967).

Tomilin (1967) describes feeding schools of Delphinus as follows: "Feeding individuals dive more deeply (than in moving schools). When they feed on stationary fish schools they dive vertically. If the school stays at a depth of 60-70 m, the dolphins chase it to the surface, where they can catch fish with greater facility. Fishermen are convinced that this animal cannot dive deeper than about 70 m because it never reached the foot rope of the "alaman"[or purse seine] which is about 70 m deep." Tarasevich (1957) suggests that if two species feed on closely similar or identical food supplies they will form mixed schools. Mixed schools are indeed evident features in dolphin schools in areas where single prey species predominate, or where a single phenomenon such as the rising of the deep scattering layer determines the food sources. For instance, in southern California waters, where either anchovy or squid schools are common prey, mixed feeding schools are common.

Dolphin species that form small or moderate size schools have rather often been reported to use more specialized kinds of

food capture patterns. For example, killer whales have been reported to work cooperatively in food capture. Andrews (1931) and Tomilin (1967) reported seeing gray whales (Eschrichtius robustus) whose tongues and flukes had been eaten or frayed by killers. Cooperative behavior in which a group of killers harried right and humpback whales being harpooned by hand whalers near shore in southern Australia has been chronicled by Dakin (1934). Some members of the killer school reportedly hung on the lips of the stricken whale while others pressed over its nostrils and still others hung on its flukes.

Killers are well known to aggregate around pinniped rookeries during pupping season (Norris and Prescott, 1961; Tomilin, 1967). The ability to find the small, isolated rookeries suggests that killer whales have considerable navigational ability and are sensitive to the seasonal variations indicating a rookery season is in progress.

One common defensive response of prey species to killer whales is to remain motionless, or in the case of the gray whale, often to turn belly up with flippers extended. The lack of motion presumably minimizes directional acoustic cues from the prey. The belly-up position of the gray whale may also allow free use of the tail, its major defensive weapon (Norris and Gentry, 1974). On first consideration, this behavior might seem to represent a submissive posture like that of a subordinate wolf exposing its throat to a dominant animal. But such subordinate behavior would seem to be of little value in staving off an attacking animal of another species such as the killer whale. Evasive

behavior is also evident, as for example by belukhas who changed river channels or avoided a river mouth altogether when recorded killer whale sounds were played in the river (Fish and Vania, 1971), or when gray whales were turned in their migration course or were caused to swim inside kelp beds by underwater projection of killer whale sounds (Cummings and Thompson, 1971).

Killer whales seem to use encirclement of large prey such as sea lions or walruses, with some regularity. Once the prey is bunched, a member or members of the killer whale group may cut through the compressed and often nearly immobile prey school, feeding as they go (Zenkovich, 1938; Norris and Prescott, 1961). Both Norris and Prescott (1961) and Leatherwood and Samaris (1974) report herding and capture of California sea lions (Zalophus californianus) by killer whales in which the whales formed a crescent behind the fleeing sea lions and raced in to make kills. Similar behavior has also been reported by Caldwell and Caldwell (1972) and Leatherwood (1975) in which Tursiops circled schools of prey fish and individuals darted through the fish schools periodically in attempts at capture.

Saayman, Tayler and Bower (1973) described the herding and crisscrossing maneuvers used by bottlenose dolphins in trapping fish schools. Busnell (1972) described an unusual relationship between native fishermen and dolphins on the west coast of Africa, in which mullet (Mugil sp.) during a near-shore migration, were herded into shallow water by humpback dolphins (Sousa teuzii) and bottlenose dolphin (Tursiop) schools. The presence

of the porpoises offshore of the fish schools allowed the fishermen to place gill nets among the fish while the dolphins also fed among the milling fish. The dolphins are reported to come to the fishing site in response to slaps of sticks against the water surface. Fink (1959) reports somewhat similar cooperative feeding of harbor porpoises in Monterey Bay, in conjunction with California sea lion schools.

Prey capture seems more often successful when the predatory cetacean forces the prey fish against a barrier of some kind, such as the surface, the shoreline or underwater formations, producing we suppose, predictable behavior on the part of the prey. This advantage has been shown by Major (1976) to exist for predatory fish forcing prey fish up against the water surface. One of us (Norris) has noted similar behavior in the Pacific bottlenose dolphins, _Tursiops gilli_. In upper Magdalena Bay, Baja California Sur, Mexico, a lone dolphin was seen working along the steeply sloping sandy shore, so close to the beach that the dolphin was turned partly on its side. Small schooling fish were periodically forced into the wedge of water along the beach whereupon the dolphin attempted capture, primarily with movements of its neck and head. A small stingray flapped completely out of the water at the observer's feet as the dolphin passed.

Schools must also be the place where young learn to feed on their own. McBride (1940), discussing captive _Tursiops truncatus_, reports that young animals would grasp fish after three weeks of nursing but that four weeks elapsed before any ingestion took

place, and eleven weeks before it became routine. Presumably in the natural environment a similar time sequence would be followed by young animals.

Optimization of Energy Supplies

Both flocking birds and herding plains-dwelling ungulates seem to follow feeding strategies that optimize food availability to the group and reduce energy expenditures needed to acquire food. Specifically, by randomization of flock or herd movements over a feeding area and by changes in density of feeding animals relative to seasonal changes in food abundance, the group is able to feed almost constantly on essentially unexploited resources, and allow the resources just utilized enough time to reconsititue themselves (seed populations build up or grass grows to optimum height for grazing). In this way the entire food resource is never reduced en masse but only randomly in part, and the difficulty of food finding is accordingly reduced to a minimum. In the sea, a human parallel is the new technique used primarily by Russian fishermen called "pulse fishing" in which a given resource area is very heavily utilized and then left to reconstitute itself while other areas are heavily fished.

The feeding patterns of some dolphins are suggestive that such a pulse fishing mechanism may be at work, especially among common dolpins, spotted and spinner dolphin schools. We will return to the circumstances in these animals after discussing one case in terrestrial animals. Cody (1971) has studied feeding in mixed desert finch flocks. He found that flocks followed random

paths ("a random walk") through a feeding area and that this behavior allowed much of the seed crop to reach full growth in the area being fed upon. The flocks were complexes of species, each member of which had a different feeding strategy and thus cropped a different part of the food supply. Differing rainfall conditions caused changed responses in the bird flocks (spreading or contraction of feeding grounds), once again tending to optimize instantaneous food availability from a finite renewable resource.

Perrin, Warner, Fiscus and Holts (1973) have discussed the multispecies feeding aggregations of pelagic predators in the eastern tropical Pacific, including schools of the spotted dolphin, the spinner dolphin, and the yellowfish tuna (Thunnus albacares). They found that the tuna and the spotted dolphin fed on fishes, squids, and crabs, largely from the epipelagic or pelagic faunas, while the spinner dolphins fed mostly on mesopelagic species. Further, the spinner dolphins in their sample showed a preponderance of empty stomachs, indicating a separation of the time of day during which spotted and spinner dolphins feed. As noted elsewhere in this paper, the Hawaiin spinner dolphin is felt to be a nocturnal feeder, while the spotted dolphin feeds during the day.

This association of tuna and dolphin is a complicated one. The tuna apparently follow the spotted dolphin schools, or as the fishermen put it: "the spotters carry fish". The bond is strong enough that fishermen can herd the dolphins with speed boats, knowing that a net set around the dolphin school is likely to

catch the fish swimming behind and below. If a mixed school of spotted and spinner dolphins is fragmented during the case the fish are reported to follow the spotted dolphins. Because of this behavior, and because the food of the spotted dolphin and the tuna are very similar, sometimes identical, it is felt that the association is probably food based.

Additional species are involved in this association. Fishermen locate both dolphins and fishes by first sighting flocks of sea birds, which include frigatebirds, boobies, terns, shearwaters, storm petrels and jaegers. The frigatebirds, which are predominant, are primarily kleptoparasitic on the food of other birds, but are also reported to us by Hawaiian fishermen to take flying fish flushed from the water by swimming predators. Jaegers, too, are kleptoparasitic. The other birds feed on aquatic prey. Additional associates are known to assemble in the water, such as pelagic sharks and billfish (W. Perrin, personal communcation).

Whether this complicated multispecies aggregation optimizes energy availability for some of its participants isn't uniformly clear. A Hawaiian fisherman reported to one of us (Norris) that he could generally estimate the size of spotted dolphin schools by the number of frigatebirds flying over them; many birds meant a large school, while a few birds were less indicative. From subsequent observations we can confirm that this numerical relationship seems generally to be true.

The spotted dolphin in its association with tuna, seems nuclear (W. Perrin, personal communication) and may assist the

tuna in daytime food finding. Both fish and dolphin are apparently feeding within 30 meters of the surface, while the spinner feeds "several hundred feet down" (Fitch and Bonnell, 1968). Thus, the spinner dolphins in mixed schools are apparently not feeding in these aggregations, and may simply orient to spotted porpoise schools during rest periods and swim passively with the other species of the aggregation, thus achieving a degree of "cover seeking" in the open sea. Insular populations seem to achieve the same degree of cover by retreating to sheltered coves or atoll lagoons.

The Hawaiin spinner dolphin feeds on scattering layer organisms off the Hawaiian Islands, and does so in a manner suggestive of randomized search. Most feeding is peformed by diving in deep water (400-2000 meters) over the steep slopes of the islands where they slope into the deep sea. After daytime rest in protected coves, schools set out to sea in late afternoon or evening, and do so in variable directions from night to night. Thus nighttime feeding apparently occurs along different parts of the slope over time. Scattering layers apparently are denser in the areas of feeding than elsewhere near the islands, and one assumes that some sort of concentrating effect upon the scattering layer is at work there, perhaps based upon subsurface currents. If so, one can think in terms of replenishment rate, and regard the use of variable feeding grounds as a mechanism allowing replenishment to occur and also, on the average, to bring the dolphins into areas of maximum food abundance along the slope.

William E. Evans (personal communication) reports a similar circumstance in common dolphins preferentially feeding over submarine escarpments in the southern California bight.

Reproduction and Growth

Reproduction

It seems probable that the proximity of individuals in a school allows reproductive synchrony to take place at less energetic cost than if animals swim alone separated by long stretches of open water, though proximity may also increase the chances of interference by sexual rivals. Seemingly, the need for mechanisms allowing location of sexually ready animals over long distances are reduced in the close confines of dolphin schools. Yet schools may sometimes be large and diffuse and the need for short range mechanisms is to be expected. The larger whales whose "schools" may cover many miles of sea may require longer range mechanisms. For instance, Payne and Webb (1971) have suggested that baleen whale schools may be spread very widely with animals often far out of visual contact, and that low frequency sounds may serve to integrate such "schools". Certainly some species such as the humpback whale (*Megaptera novaengliae*) seem to produce complex calls largely or wholly on the breeding grounds and are mainly silent when at other places. However the right whale (*Eubalaena glacialis*) produce complex "stanza calls" far from calving areas (Cummings, Fish and Thompson, 1972). The calls of baleen whales may travel many or even two hundred or more kilometers

at sea, and clearly could serve as a means for localization of mates. In the more cohesive schools of dolphins and toothed whales such mechanisms are doubtless functional over much shorter ranges and it is possible that such special reproductive calls as that described by Dreher (1966) are effective in organizing reproductive activity within schools, though Caldwell and Caldwell (1972) regard such signals as primarily related to individual identification, and not specifically assignable to the circumstances of reproduction.

In the first few days of life many newborn cetacenas, especially delphinids, may engage in echelon swimming (Norris and Prescott, 1961), a swimming posture in which the baby animal positions itself above the midline forward of the dorsal fin of its mother. It typically lies against her side without swimming movements as she moves through the water. Dohl, Norris and Kang (1974) report for a roughtooth dolphin-bottlenose dolphin (_Steno bredanensis_ x _Tursiops truncatus_) hybrid that the young animal performed this maneuver only when it actively pressed its inboard pectoral flipper against the mother's side (Figure 3). Such behavior may be the basis for reports that female belukhas carry their babies on their backs (Chapskii, 1941).

While location of potential mates represents the first level of discrimination needed for successful reproduction, a more refined level concerns detection of sexual readiness. Such detection can reduce the energetic cost of the reproductive process and contribute to the precise timing of reproductive events. In migratory species at least, such timing would seem of crucial

importance, and is probably generally assisted by a photoperiodically mediated timing mechanism (Dawbin, 1966; Clarke, 1957; Norris, 1967)(Figure 4).

In general, as with terrestrial animals and birds, sexual timing seems most precise in migrators, and in species or populations living in seasonal climates where both light levels and temperature may undergo strong seasonal fluctuations. This is not to say, however, that many tropical terristrial animals may not have precisely timed reproduction. Tropical and subtropical cetacean species generally seem to exhibit very broad modes of reproduction spread over many months (W. F. Perrin, 1970, 1972, and personal communication, for Stenella attenuata and S. longirostris; Evans, 1975, for Delphinus; Tomilin, 1967, for Delphinus delphis, in the Black Sea). Tarasevich (1957) suggests that seasonality in reproduction insures segregation of pregnant females and young within dolphin schools since sexually mature males do not participate in training of or caring for the young.

Gilmore (1961) has suggested that gray whales might locate lagoon mouths or follow one another by taste during migrations. It seems an important possibility that schooling animals, such as most porpoise species, may indicate sexual readiness by specific tastes imparted to the water through which the school swims (see Caldwell and Caldwell, 1967). This point was brought home with some force to us (Norris and Dohl, ms) when observering spinner dolphins from an underwater viewing vehicle. We found that these animals possessed a well-defined defacation period

during which the water was literally filled with olive-colored trails of finely divided fecal material. This period occurred for a few hours in the morning, after a night's feeding, and before the usual midday rest period. An impressive feature of this activity was that most school members swam through such clouds of material. Urination, which is probably a nearly constant process in cetaceans, may provide chemical cues about or to sexually ready animals. If indeed such a mechanism exists, the school is clearly useful in promoting successful mating.

Sexual readiness is otherwise evident in dolphins. For instance, changes in the shape and color of the genital area in porpoises entering sexual readiness have been reported (Tavolga and Essapian, 1957; Tayler and Saayman, 1972). Behavioral cueing systems are obviously important too, in refining timing of mating (Tavolga and Essapian, 1957).

Some odontocetes, such as killer whales, pilot whales, sperm whales and other strongly dimorphic forms, seem to be uniformly polygynous, with relatively few adult males, or even a single male in schools having many females or immature animals. Sergeant (1959) regards this as the inevitable consequence of higher mortality in males, resulting in sex ratios greatly different than 1:1. Pelagic dolphin species that are not highly dimorphic, such as the common dolphin of the Black Sea are reported near to 1:1, or actually slightly biased in favor of males. Among 82,843 specimens examined. 53.6% were males and 46.8% were females, with very similar figures being

recorded for embryos taken (Tsalkin, 1938).

Sexual segregation occurs commonly in dolphin schools. Norris and Prescott (1961) report it for northeastern Pacific pilot whale schools in southern California waters. True (1890) reports it for *Tursiops truncatus* in samples taken by the Cape Hatteras seine fishery, and many other examples could be cited for other genera.

Intraspecific scarring, often sexually related, is widespread in odontocete schools. Dolphins and toothed whales commonly rake one another with their teeth, and from spacing and number of such marks it is often possible to assign the marks to schoolmates (Norris, 1967). A subadult female Cuvier's Beaked Whale (*Ziphius cavirostris*), for instance, bore marks of the two teeth of an adult male of the same species (Norris and Prescott, 1961)(Figure 5). Gunter (1943) reported a high incidence of scarring in males of *Tursiops truncatus* in Texas bays. Norris and Prescott (1961) cite observations of eastern north Pacific pilot whales in which juvenile males were usually covered with scar marks from larger animals, while adult males were largely without scars from conspecifics, presumably having healed completely during growth. Sex and age segregated sperm whale schools are commonly reported (see, for example, Clarke, 1957). Nursery herds of mothers and young numbering 100-150 animals have been reported in the Mozambique Channel, with such schools staying in water warmer than about 17°C. Males, on the other hand, may penetrate into polar regions (Caldwell, Caldwell and Rice, 1966).

At any rate, sexuality seems likely to develop extremely early in schooling porpoises and certainly plays a central part in play and in social ordering of the school (Bateson, 1965). Erections and sexual play begin very early in dolphin life. Caldwell and Caldwell (1967) report a newborn Tursiops having an erection at the age of two days when brushed by its mother.

Pregnancy and parturition are also involved in social ordering within the school. McBride and Kirtzler (1951) present evidence that when pregnant female Atlantic bottlenose dolphins are about four months from term they may segregate themselves from their normal position in the social order of the school. Swimming activity tends to slow, and during contractions, a peculiar "yawning behavior" was seen and a unique bark was heard. And, after birth, the females and her young were often subject to savage attack by the adult males present, behavior which in wild schools would clearly result in structuring of the school. In fact, since such behavior is confined by tank limits in captivity what seems to be destructive behavior might in fact be adaptive, perhaps resulting in the locations of females and young within the center of the school, as has often been observed. The attacks may represent herding. Structuring would be enhanced further by the circling behavior and whistling (McBride and Kirtzler, 1951) which allows the mother to locate young animals that have strayed even though widely separated. In the same captive school it was noted that when danger threatened, "Auntie Dolphins" (female consorts of the mother-young pair) rushed to them, and the school as a whole tended to coalesce around them.

A commonly observed feature of dimorphic odontocete schools is the positioning of adult males on school wings, with mothers and young more centrally located. This feature is sometimes strikingly evident in killer whale and pilot whale schools. On December 7, 1971, while the authors were on board the research vessel Alpha Helix on a cruise under the scientific leadership of Dr. Gerald Kooyman, a school of fifteen killer whales was encountered and followed for six and a half hours. The school was continually harrassed by the vessel and yet it consistently maintained its structure -- the adult males on the wings of the rank-shaped school with what were presumed to be females and young in the central position, or sometimes as a subgroup behind the middle region of the school. The school as a whole maneuvered constantly to elude us and yet this form remained. It was a striking exhibition of the cohesiveness of this aspect of school formation, and was made clearly evident to the observers by the extreme dimorphism of the animals. It is interesting to consider this structure in relation to the selfish herd hypothesis of Hamilton (1971) which shows that animals on the margins of schools are more vulnerable to predation than interior animals. In the very dimorphic species discussed above it seems obvious that the very large males should be less subject to predation than the smaller females and young and hence dimorphism should, to some degree, compensate for exposed position in males.

A unique roseate formation has been described for sperm whales by Nishiwaki (1962) in which several whales lie at the

surface facing each other, positioned like the spokes of a wheel. This behavior has also been noted by E. Barham and W. E. Evans (personal communication) during an aerial survey in the eastern tropical Pacific. Its function is unknown.

A number of reports describe sweeping changes in school structure related to sex or reproduction. Unisexual schools have been reported to occur under certain circumstances by a number of authors, usually during migration. A few examples will suffice. Pregnant female common dolphins in the Black Sea may migrate offshore to calve but yet remain within the general confines of the very large and spread schools (Tsalkin, 1938). The belukha regularly segregates into a unisexual school during migration, adult males generally forming a vanguard while females and young may travel behind (Arsen'ev, 1939). The narwhal (<u>Monodon monoceros</u>) likewise forms unisexual schools at times, including migratory groups in northern Canada in which adult males may go on entirely different migratory paths than remaining portions of the school (Newman, 1968).

Ohsumi (1971) has reported on an interesting experiment concerning school composition of sperm whales. An attempt was made to catch all members of nursery schools which occur in certain localized areas, and three such schools were taken. Examination revealed that average school size was 27.1 animals, males were all calves and represented 22.9% of the schools, with adult females and female calves comprising the remainder. Males are reported to leave these schools at puberty to form "bachelor schools". Bulls are thought to struggle with one

another to assume a position in "harem schools" during the breeding season. Ohsumi regards the harem as temporary, and males are often seen as solitary animals at other seasons. In nursery schools Ohsumi feels leadership is exercised by old females, though all-male groups apparently lack a leader.

Periodic coalescence of smaller schools into larger aggregations during parturition has been reported for the common dolphin in the Black Sea by Tsalkin (1938). Similar behavior was noted by the authors for the Hawaiian spinner dolphin in which aggregation of most or all schools of spinner porpoises living on the lee coast of the Island of Hawaii was noted in early fall at a time when births were especially common, though birth was far from restricted to this period, but instead spread rather widely through the year.

Such aggregations may provide more than protection. For instance, Brown, Caldwell and Caldwell (1966) refer to schoolmates assisting in the removal of the afterbirth from a newly parturient mother, and Dohl, Norris and Kang (1974) report similar though incomplete behavior in the rough-tooth dolphin (Steno bredanensis). Aggregation on breeding grounds is probably both best known and most restricted geographically for the gray whale, the black right whales (Eubalaena glacialis), and the humpback whale (Megaptera novaeangliae) which gather for calving in inland lagoons or along island shores. Clarke (1957) suggests that such aggregation enhances reproductive success and that it played an important part in allowing such populations to recover from near extinction, at least in the case of the gray wha

Growth

Often the growth stage of cetaceans seems to regulate their location within a school. As has been discussed above, mother-young pairs are prominent features of cetacean groupings (Figure 6), and such pairs may persist on an intermittent basis for remarkably long periods. For example in the Atlantic bottlenose dolphin the members of a mother-young pair may return to each other in time of stress for years after the young has reached adulthood (Tavolga and Essapian, 1957). Infants often remain near their mothers during capture (Gunter, 1943). For example, whalers sometimes caught young sperm whales because the mother, and sometimes other schoolmates, were attracted to the captive and could be killed (Caldwell, Caldwell and Rice, 1966). Mal'm (1938) reports that female common dolphins whose infants have been killed in nets may swim about them in spite of nearby fishing activities.

Yet is is also a common observation that juvenile animals may be found throughout a school, and that very small young may sometimes actually swim in the lead of spinner dolphin schools (Norris and Dohl, ms). This observation, we feel, does not indicate actual leadership in the school falling upon the young, but instead the lack of any such defined leader in the school. Half grown spinner dolphins have been noted performing repeated spins at the advancing front of a school travelling to the feeding grounds after completion of a rest period, yet when the same school changed direction 180° these animals were at once part of the trailing group.

That dispersal, especially of juvenile whales, may occur over wide areas, and thus influence genetic intermixture, is indicated by tagging results from Antarctic baleen whales (Brown, 1954) which showed as much as a 50° longitudinal dispersal in fin and blue whales. Such dispersal occurred rapidly according to tag returns. Whether such dispersal movements are features in other species, as they are in some terrestrial and avian species, is unknown.

Dominance hierarchies are known from captive odontocete schools, and reflect, to some degree, age structure within the schools [see for example, Tavolga and Essapian, 1957; McBride and Hebb, 1948 (both for Tursiops truncatus); Norris and Prescott, 1961 (Globicephala scammoni); Bateson, (1956 (Stenella longirostris and Stenella attenuata)] and they in turn affect the overall structure of schools. For instance, McBride (1940) reported a well-defined size-related order in captive Tursiops truncatus schools. New arrivials were first bitten by established males and females. After a few weeks such newcomers were assimilated into the established schools, though some seemingly permanent intimidation seemed to exist, signaled by jaw claps and a peculiar body posture "like that taken by a dolphin preparing to get underway."

In natural schools at sea dominance may be expressed largely by spacing and placement of subgroups and by sexual segregation within the school as a whole, while in captivity confinement may convert such dispersive pressure into the establishment of hierarchies. Thus one should be careful in interpretation from

captive observations to the conditions which might be supposed to occur in nature.

Social Integration and Communication

A considerable body of anecdotal evidence can be mustered showing that odontocete schools function to allow social integration, and some of it has been mentioned in earlier contexts. In fact, one can conceive of the school as an equilibrium system ordered by two sorts of social phenomena: those factors tending to promote cohesion of the school and hence to bring school members together, and those factors that tend to spread the school apart. These two composite phenomena have been called "centrifugal" and "centripetal" factors by Breder (1954). Indeed, it is notable that dolphin schools, in general, change drastically in size, and also change the spacing of animals and subgroups under differing conditions. For instance, spinner dolphins are highly aggregated during daytime rest periods; in fact, the animals swim so closely packed that some members may be near to touching (Bateson, 1965, reports that sleeping animals do not actually touch in mixed Stenella schools), and groups of as many as fifty animals may occupy an area no larger than 40-60 meters in diameter. The same school may assume a spread formation later in the day and evening, during feeding, and may spread over a kilometer of sea, with subgroups and even individuals widely spaced.

The parts of such a social integration system are obviously diverse. We can, however, list some phenomen or patterns that

tend toward cohesion, and those than tend to dispersion. Patterns tending toward cohesion seem to be involved with protection, fright, sleep or rest, and familial or habitual associations. Patterns tending toward dispersion seem to be involved in alertness, aggression, feeding, and a lack of familial or habitual association.

Such social integration is obviously mediated by various sensory and signalling systems. It seems clear that vision and hearing and perhaps taste are the most important for most cetaceans. The many examples of cetacean reactions to sounds do not need to be recounted here. Suffice it to say that ample evidence exists that sounds, either produced by the animals themselves or from other sources in their environment, serve many vital functions. It is probable that most unified actions of schools when spread over considerable expanses of water are acoustically mediated. For example, flight, synchronous diving in conditions of low visibility, epimeletic behavior in which school members may come from considerable distances to assist distressed members, feeding behavior in which cetaceans may swim long distances to specific feeding situations, synchronized intraspecific school movements, and probably migration and avoidance of stranding in areas of great tidal fluctuations, are apt to be assisted by phonation, passive listening, or active echolocation. McBride and Hebb (1948) presented some of the first well documented examples of these sorts, and Tomilin (1955) expanded these questions further.

Epimeletic behavior, mentioned above, is especially afforded female and young animals, adult males often being left untended though in distress (Hubbs, 1953). Such behavior is very widely known amongst odontocetes and is also known from some mysticetes (Caldwell and Caldwell, 1966)(Figure 7).

It is likely that protection of individual cetaceans, especially small ones, is greatly enhanced by being in a school, just as has been shown to be the case for fish (Breder, 1967). In fact, for an oceanic dolphin the school represents the focus of all living activity and lone animals at sea tend to be severely frightened. This graphically shown in early tests using single trained dolphins to work in the open sea (Norris, 1965).

Fright induces bunching of dolphin schools, often of a very extreme sort. Animals may come in close contact, or perhaps are actually touching at times in a dense fleeing school. If a school is disturbed and pursued, and if great disturbance is caused, as by a shot fired into the water, the animals will come together, and usually will begin rapid synchronized swimming away from the disturbance, often accompanied by frequent leaps. Roughly, the greater the fright, the tighter the school may become, and the more time it may spend leaping.

MacAskie (1966) reported on the peculiar behavior of a school of killer whales which had been "cornered" against a sea cliff by three vessels. All five animals reared bolt upright in the water with their heads facing offshore toward the encircling vessels. They then dove and appeared on the sea side of the vessels and disappeared.

Perhaps no other group or school behavior in cetaceans has excited such controversy as mass stranding. Many species of cetaceans have stranded as single individuals, and these seem uniformly ill, but whole schools of certain species strand *en masse* [especially Globicephaline whales, killer whales, false killer whales, their near relatives the electra (*Peponocephala electra*) and the pygmy killer whale (*Feresa attenuata*)] and some such strandings seem to include non-moribund individuals, since members of such schools have sometimes been kept alive in oceanaria, while it is rare for single strandings to recover (Figure 8). A number of theories designed to explain this perplexing behavior have been advanced. In most cases the most logical cause seems to be that for a variety of reasons, such as faulty navigation, parasitism or disease (especially of the nervous system), a single animal or the majority of the school may strand and the remainder may come onto the beach because of factors relating to the tight social integrity of the school, probably mediated by acoustic and other signals (see Norris, 1967). Most of the major stranding species are members of groups in which pronounced sexual dimorphism and organized school structure are known (though other nondimorphic genera such as *Lagenorhynchus* also strand occasionally). In fact, pronounced sexual dimorphism is almost confined to odontocetes species that regularly strand as schools.

Sleep or rest in natural schools has seldom been observed. It has been noted in the spinner dolphin (Norris and Dohl, ms.), the common dolphin (Evans, 1974), and the northeastern Pacific

pilot whale (Norris and Prescott, 1961). Some observations on captive animals have been made; for example, sleep groups are reported for the Hawaiian spinner and spotted dolphins (Bateson, 1965). Occasional records by whalers of quietly floating animals that could easily be approached, or which were run into by the whaling vessel, have sometimes been described as sleep. For example, the Greenland or bowhead whale (Balaena mysticetus) has been encountered in this fashion (Gray, 1887), as has the fin whale. McBride (1940) describes similar nearly motionless sleep in captive Atlantic bottlenose dolphins, in which animals sculled slowly with eyelids closed, except for a brief opening every 15 seconds or so.

Social order may be altered between sleep and active states, with subgroup size changing and shifts in social grouping also taking place (Bateson, 1965; Caldwell and Caldwell, 1964).

The typical sleep pattern seems to consist of marked aggregation of school members, slowing of swimming, changes in diving rhythms, and a suppression or alteration of normal familial and habitual association patterns (see Slijper and van Utrecht, 1959). As mentioned earlier, in the Hawaiian spinner dolphin rest seems usually to occur near midday, and to occur in insular populations in sheltered coves or atoll lagoons. Rest behavior in oceanic spinner dolphin populations remains unobserved, but, as noted elsewhere, may take place with other porpose species. In insular spinner dolphins typically a school will come inshore in rank formation, showing subgroup structure, from feeding grounds in deep water, and much activity such as spinning,

leaping, and head slapping will be seen. Once in the rest area the school tends to slow and become discoidal, very tightly packed (to or near the point of actual contact of members) and aerial behavior soon ceases altogether. Diving, which is shallow in the travelling school, becomes predominant, with surface times reduced until only a few breaths are taken before resubmergence. Phonation changes from a varied mixture of squeals, barks, whistles and clicks in the travelling school to desultory click emission in the resting school. Powell (1966) has described a similar diurnal pattern of phonation in Tursiops, with peaks in the morning and afternoon (Figure 9). Arousal in the resting spinner dolphin school may first be noticed either by a resurgence of phonation or aerial behavior (Norris and Dohl, ms.).

Familial or habitual associations are known to be prominent features of bottlenose dolphin schools (McBride and Hebb, 1948; Tavolga and Essapian, 1957; Caldwell and Caldwell, 1964; Tavolga, 1966). While familial associations are essentially unknown for other odontocete species because captive schools have not been available for study over long enough periods, anecdotal evidence suggests that the general pattern found in the bottlenose dolphin is probably very common throughout the Odontoceti. That is, we expect that familial or habitual groupings exist in most, or perhaps all, odontocete schools. The only possible exception that comes to mind is the rather solitary susu (Platanista gangetica) which is usually seen alone or in pairs (Kasuya and Aminul Haque, 1972). The presence within most odontocete schools of stable associations such as mother-young pairs, and age and

sex groups supports this.

Casual groups of various species are often assembled in oceanaria and when studied, are found to have developed social relationships usually involving all captive species (Figure 10). Bateson (1965), observing such an assemblage of spinner and spotted dolphins, noted specific groups of the two species into dyadic and triadic associations, with most sexual behavior occurring between species (Figure 11). A complex hierarchy of threat signals was also noted, involving both species. Brown and Norris (1956) reported that interspecific matings or mating attempts occurred nearly daily between a male bottlenose dolphin and a North Pacific striped dolphin. Brown, Caldwell and Caldwell (1966) reported on behavioral interactions between a false killer whale (Pseudorca crassidens) and a pilot whale (Globicephala scammoni) and between North Pacific striped dolphin-bottlenose dolphin pairs. This intergeneric activity included sexual behavior, behavior during parturition and strong social attachments. In fact, broadly speaking, odontocetes in captivity seem to be able to construct social groups from species which may be widely divergent phylogenetically and morphologically. An extreme example of this sort was the remarkable imitative social and sexual behavior noted by Tayler and Saayman (1973) between an Indian Ocean bottlenose dolphin (Tursiops aduncus) and a Cape fur seal (Arctocephalus pusillus).

A similar association between widely divergent marine mammal taxa has been noted by Norris, Goodman, Villa-Ramirez and Hobbs (in press) in which California sea lions were seen associating

closely with courting and mating California gray whales at the entrance to a calving lagoon. The sea lions, all subadult animals, swam closely among the whale groups, and followed them as they moved. The basis for this association is unclear.

Most interesting and challenging, it seems to us, is the potential contribution of learning the contingency patterns of communication to school behavior and structure. Such second order learning (see Reusch and Bateson, 1961) opens the way for much subtlety of behavior. With it communication may become a conscious process for both sender and receiver, rather than the perhaps more usual mammalian pattern in which an emotional state in one animal is perceived by another and reacted to without the sender necessarily knowing it had transmitted signals in the first place. The way becomes open to the use of ideas, however simple. Ideas are, after all, second order abstractions themselves. Was the case of the false killer whale and the Pacific bottlenose dolphin discussed by Pryor (1973) of this sort? These animals, kept in adjoining tanks, learned to join each other by the more agile bottlenose dolphin jumping the barrier between the two tanks in which the animals were held. When trainers sought to contain them by increasing the width and height of the barrier the dolphin was no longer able to leap it, but the whale, with its superior strength, repeatedly and apparently covertly pushed the barrier aside enough for the dolphin to jump in. As with most anecdotes we are left unsatisfied, but together with experimental evidence cited earlier it seems a fertile area for study. With such contextual capability

as part of the behavioral armament of the dolphin in a school we might expect to find a number of advanced patterns involving behavior based on ideas. One might find evidence of altruism resulting from behavioral transactions in which the context might be widely known. Assistance or support behavior of cetaceans has commonly been observed and is clearly altruistic. (Caldwell and Caldwell, 1966). Examples have been observed both in captive and wild animals, and are sometimes inter-specific. For instance, a north Pacific striped dolphin died in an oceanarium tank, and as it sank to the bottom an adult Atlantic bottlenose dolphin attempted to raise it in typical supporting behavior (Brown and Norris, 1956). Two additional examples are provided by Norris and Prescott (1961) and Caldwell, Brown and Caldwell (1963). In the first example a distressed Dall porpoise, which had just been introduced to an oceanarium tank, was supported by two North Pacific striped dolphins, and in the latter, an adult male Northeastern Pacific pilot whale carried a dead Pacific striped dolphin for many hours in an oceanarium and resolutely prevented the staff from removing it from the tank. An example of intergeneric "standing by" behavior was noted during the capture of a Northeastern Pacific pilot whale, in which the whale was accompanied throughout capture by a group of Pacific striped dolphins, which left the collecting vessel only after the whale was hoisted on board (Norris, 1974). The smaller dolphins swam very close to the tethered whale during the entire half hour of capture. One wonders if the rather frequent reports of dolphins supporting

people at sea are of this sort. At any rate, the question arises from such examples whether the animals were responding by means of a fixed action pattern to the "distress signals" produced by the stricken animal, or whether the animal involved in epimeletic behavior had perceived the context of the situation (i.e., distress and the imminent possibility of death) and was able to react to it.

Because of the experimental evidence for second order learning in dolphins we do not think the latter explanation can any longer be cast aside on grounds of parsimony. So far as we know, no other animal other than man will come to the assistance of a distressed member of another taxon.

Altruism, and its relation to ideas of group selection has received much attention recently by students of evolution (see, for example, Lewontin, 1970), because true altruism between non-interbreeding forms may be difficult to explain without resort to selection at levels of relation more distant than kin groups. This we feel may sometimes be a misleading simplification. Cetaceans seem clearly to exhibit intergenetic or even interfamilial altruism. The basic pattern of epimeletic behavior, however, must be used largely intraspecifically, and the examples given most likely represent "spill over" of an intraspecific pattern into the domain of more distant relationships. Selection operates by compromise and balance in a systemic sense, with other traits of the evolving species, and even though the trait of supporting schoolmates in distress is valuable to the species, the complex of signals, cognitions and

response that it entails may allow it to be expressed by one cetacean to another, even though they may be reproductively isolated. The more interesting question, it seems to us, is whether or not it represents a contexual response to a common circumstance.

Evidence of distress is typical of the giver of epimeletic behavior. The pilot whale mentioned above, during its support of the stricken Pacific striped dolphin, was highly agitated, as could be seen by the widely opened eyes, with whites showing (Caldwell, Brown and Caldwell, 1963). In another example, an Atlantic bottlenose dolphin carried a dead leopard shark for 8 days, avoiding all attempts to take the shark from her, and was nearly inappetant the entire time. Once the shark was finally removed the dolphin returned quickly to a normal feeding pattern (Norris and Prescott, 1961).

That individual or species recognition is of great importance in the social integration of dolphin schools is probably indicated by the observation of Perrin (1972b) on the dimorphism of the eastern tropical Pacific spinner dolphin. He found that bizarre dimorphism of the dorsal fin and post-anal protuberance exists in the species only in the tropical eastern Pacific, even though the species is probably pantropical. Only in this area of Pacific in which extreme dimorphism is found is the species known to travel regularly with other genera or species, such as Stenella attenuata and Delphinus delphis. Thus, the supposition is that heightened intraspecific recognition systems are necessary.

Sensory Integration

Sensory integration, we believe, is an extremely important function of the dolphin school, just as it seems to be for fish schools (Shaw, 1969). By this we mean that the school serves to integrate the sensory inputs of many members of a school to provide environmental information to part or the entire school. For example, an incoming sensation of danger by one or a few animals can quickly transmit through the school and result in appropriate evasive or aggressive action. This is clearly true in dolphin schools since harrassment of one part of a school will often cause the school as a whole to react. That is not to say that the school may not fragment, especially if it is large, and come to form two or more subschools. It is a common observation that such is the case. The parts may or may not rejoint after the disturbance has ceased.

Sensory integration thus provides to the individual animal the integrated sensory capability of many animals sensing in many different loci and directions. Presumably much sensory input of this sort is acoustic, either from active echolocation or passive listening, though other sources of data such as vision, taste, temperature sensation, tactile sensation, and possibly other modalities are likely to be involved. For instance, the commonly observed echelon formation of the animals in cetacean school subgroups may be a function of turbulence patterns generated by adjacent animals (Breder, 1965). Not only does sensory integration provide individuals with increased environmental information, but as a result it frees them for other activities within the

school. A dolphin in a school engages in many kinds of social activity such as sexual behavior (Figure 12), play, familial interchange of various sorts, in addition to sensing the surrounding world. In fact the level of intricacy of social activity is likely directly dependent upon the reliance the animal may put upon its security within the sensory integration system of the school. Thus sensory integration is basic to other school activities; in essence it provides a high level of environmental awareness at modest individual expense. The school thus becomes a moving enclave of safety within which the animal is free to engage in other activities. In this sense it serves some of the functions generally ascribed to "home range" and "territory" for terrestrial animals.

Examples of such sensory integration have seldom been mentioned in the literature. Norris and Dohl (ms.) describe the movement patterns of resting spinner dolphins in what seems to provide a clear example.

"The resting school moved slowly back and forth ranging from a few meters off the cliff face to perhaps 250 meters offshore. It travelled slowly, mostly underwater, rising in a tight discoidal group for four or five quiet breaths before submerging again. The animals rose rather steeply to the surface, not as a single tightly integrated group, but seriatum, as a column of animals. Often after rising the animals spread outward from this rising column a short distance before turning to define the compact confines of the school, like the petals of a flower opening. Such schools seem to be without striking

subgroup structure in that animals seem much for equidistantly spaced than in alert schools. To be sure, some bunching could be discerned but it was much less evident than in feeding or travelling groups, and done with deliberateness. Such groups, though seemingly less alert than moving schools, were found to be exquisitely aware of any strange objects, such as buoys, boats, lines or swimmers in their environment. It was striking that they reacted to such foreign objects in much the same way as we have come to expect from groups of schooling fishes, and not with typical dolphin individuality. For instance, when such a school cruised along the shoreside of the point where we waited in a quietly rocking skiff some 150 meters offshore, the school approached slowly as a discoidal group, thinned as it reached a point directly inshore of us, streamed between the skiff and the cliff as a long line of quietly moving animals and reformed its discoidal shape once past us. We found that our skiff or our anchored workboat could deform such discoidal groups from some distance, causing the side nearest the skiff to become dented or malformed as the entire school reacted to our presence. When a four hydrophone array capable of triangulation by sound was placed near the path of such resting schools it was assiduously avoided and no animals passed through it (Watkins and Schevill, 1972). A line stretched across the water was capable of deflecting such schools. In all of these cases, even though the animals moved slowly and other evidences of alertness such as complex phonation or aerial behavior were suppressed, the school as a whole remained alert, through sensory

integration we suppose, and was even more aware of strange circumstances in its environment than obviously alert schools. For instance, it is usually possible to cruise among alert schools and many school members will station at the bow within a few feet of the observer, but resting animals never allow this privilege but move away in the manner of a fish school."

Shaw (1969) cites an interesting correlative observation in fish, in which a frightened school with erratic schooling behavior was tranquilized en masse causing schooling to become at once "more precise and classical". Thus it may be that these observations indicate that dolphins, at least, may normally exist in their schools at a higher level of social integration and complexity and descend to a simpler level of school integration during sleep or rest. In the case of frightened fish, however, what superficially looks like the less regular alert dolphin school may, in fact, represent a breakdown of the normal constraints producing tightly integrated schooling.

A number of other possible examples of sensory integration mechanisms are known for cetaceans. Layne and Caldwell (1964) mention the existence of rheotaxis in the boutu of the Amazon River, and one wonders if this orientational method might not in part, regulate swimming patterns for entire schools of this riverine species.

Vocal signals are, of course, common in dolphins and whales, and within the framework of the school may serve to integrate school activities as a whole (see, for example, Brown, Caldwell

and Caldwell, 1966, who report incessant vocalization in travelling false killer whale schools). McBride (1940) first reported that variations in whistle types were related to emotional state, an observation which has often been repeated since. What are termed "distress calls" have been described by Lilly (1963) as a two-part whistle of rising and falling inflection. However, it has proved difficult to assign such a context to the call with security as F. G. Wood (in Norris, 1966, p. 542) points out, since distressed animals may not always emit it, and since similar calls may be given when no distress is evident. The stereotypy of dolphin whistles to individual animals (signature whistles) and of what is called a distress whistle is especially emphasized by Caldwell and Caldwell (1972) who report such signals being emitted under a variety of emotional states by many animals. Nonetheless, a repetitive call of this sort is often heard during capture sequences from the captive animal (other schoolmates are typically silent at such times) or in stressed animals in captivity.

The spin of spinner dolphins consists of a leap from the water accompanied by a rapid rotation along the longitudinal axis causing a cavity to be scooped out of the surface upon reentry (Figure 13). Hester, Hunter and Whitney (1963) have described the spins as most prevalent in slowly moving schools, and to be performed by both adults and young. We (Norris and Dohl, ms.) concur and report that they are most common when animals are in spread formation. Such conditions occur especially during

during nighttime feeding. We have also been able to record the sound produced by such spins and to plot the frequency of spins throughout daylight hours, finding they were most prevalent at dusk. We propose that such spins may provide a short range omnidirectional sound signal (in comparison with the highly directional and probably longer range forwardly directed biosonar beams) useful in defining the positions of schoolmates when vision is ineffective. Spins are very common at night, as we know from captive observations, but we have not been able to quantify nighttime frequency in nature.

Another possible sensory integration system may be found in the visual assessment of the pattern of one animal by another. It is known for birds, for example, that the remarkably precise formation flight of shorebirds such as sandpipers may be assisted by mutual observation of the color patterns of adjacent birds (Diana Tombach, personal communication). Both birds and dolphins typically show a dorsoventral partitioning of pattern. Both are generally dark above, but often with important contrasting pattern components such as wing specula or patterned dorsal fins. Both typically show a differentiated lateral pattern, often with dark lines or blotches, and both typically show ventral light patterns often demarcated from the pattern above by longitudinal dark markings. Also, both forms often show pectoral contrasting markings that may be differentially shown when a limb is moved (Figure 14). That is, in the preparation for banking flight or during maneuvers when swimming, an animal may lift a limb, showing the contrasting pattern mark in

greater or lesser degree. Distinctive axillary marks are known in dolphins, as for example, in the tonina, Cephalorhynchus eutropia and the llampa, or Peale's dolphin, Lagenorhynchus australis.

In either the dolphin or the bird, as school or flock-mates commence changes in direction such as dives, wheeling movements, or leaping, the intention is probably very rapidly communicated to adjacent schoolmates by visual changes in these pattern components. In the case of birds high speed photography has shown that such directional changes, even though appearing simultaneous to a human observer, are indeed progressive changes throughout the flock, indicating that animals across the width or length of a flock are reacting seriatum to changes in direction initiated at some locus in the flock. The same system may well operate in dolphin schools to integrate school movements during feeding, flight or at other times when movements coordinated between individuals are of special value.

Doubtless schools act upon information from the physical as well as the biological environment. Passive listening to waves, or rheotaxis may give excellent cues for orientation in tidal situations such as are regularly encountered by all estuarine or shore dwelling species. In general, these species are obviously fully aware of tidal changes and the complexities of changing channels in shoaling water. True (1885) mentions movements of schools of Atlantic bottlenose dolphins in and out with the tide, as does Gunter (1943). Gray whale mother and young pairs must constantly deal with such problems in their

shallow calving lagoons, and many young seem to be lost to tidal stranding (Eberhardt and Norris, 1964; and Norris, Goodman, Villa-Ramirez and Hobbs, in press) indicating that learning is involved since adults seldom strand and seem to have learned to cope for themselves as well as their young when the two remain together. Changing light levels and spectral quality related to shoaling water around oceanic islands may give rather precise indications of depths to marine animals (Norris, 1974).

The fin whale, which is usually an open water species, strands with some regularity. In the Sea of Okhotsk, Middendorf (1869; cited in Tomilin, 1967) reports fin whales being commonly trapped on certain muddy shoals where large tides create bars during tidal recession.

✓ Pilleri and Knuckey (1967) speculate that sun naviation is the basis of regular movements of common dolphin schools in the Mediterranean Sea. The schools move into the sun in the morning, reversing direction in the afternoon, once again moving into the sun.

Learning

The highly developed learning capabilities of odontocetes are well known from work with captive animals (Kellogg and Rice, 1966; Pryor, Haag and O'Rielly, 1969; Herman and Arbeit, 1973; and see Chapter of this volume). As in the case with other higher mammals, this seems clearly to translate into the greater importance of learning in the social patterns of odontocetes

than in lower mammals. The school is the social unit within which such learning must find its meaning. Enough examples of intraschool learning are known to surmise that it may be of major importance in the integration and expression of school functions. Further, learning during maturation must depend to a considerable extent upon feed-back relations within the school. Young animals must learn the right things at the right time (Eibl-Eibesfeldt, 1967) to fit such learning into the proper context of dolphin life and growth patterns as a whole.

Examples of learned behavior in dolphin schools are well known. It is a common observation that dolphins will learn to recognize vessels that harrass them and will selectively avoid such craft (Norris, 1974). For example, harrassment of a 30 ± spinner porpoise school on the lee coast of Oahu by collectors resulted in avoidance of the collecting craft. The avoidance lasted for more than a year. Its inception took approximately the following pattern: the first and second animals were rather easily netted from the school. However, when a try was made for a third, avoidance took place. The collector, suspecting his motor noise was alerting the animals, came in upon them at widely different engine speeds than he had customarily used and was able to net a third. A fourth animal was taken by masking engine noise with an auxiliary generator engine, but no further animals could be taken from that ship. The avoidance was probably reinforced from time to time by the collector who periodically attempted to approach

experienced animals. After several attempts to net bottlenose dolphins in San Diego Bay, the Marineland of the Pacific collecting vessel Geronimo was avoided, even though the same school was noted riding the bow of passing vessels such as harbor tugs and merchant craft (Norris, 1974). In large schools, avoidance of collecting vessels may not come to involve the entire school, even though repeated collections are made from it. This was the case with a spotted dolphin school which ranges along the Oahu Island shore (Hawaii) on both sides of Kaena Point. Over five years time more than a dozen animals have been collected from this school. It appears in this case, that a given capture increased the skittishness of some animals in the school but that other parts of the school remained approachable by the collecting vessel. This school numbers an estimated 250 animals. It may simply be that the fear of individual experienced animals translates to school avoidance in small schools while in larger ones it does not.

School behavior seems rather often to be modified by learning in special feeding situations. In some cases where relatively transitory human patterns are also involved one can be sure that learning is important in the dolphin's behavior. Two examples of this sort are presented by Norris and Prescott (1961) for the Pacific bottlenose dolphin. The first example concerned the rather regular attendance of a school of bottlenose dolphins at the Navy garbage station, located off Imperial Beach, California. On a regular schedule, the Navy gathered garbage from Navy ships at anchor in San Diego Harbor, and

transported it out of the bay and some kilometers down the coast to the dumping location. A bottlenose dolphin school, normally seen inside or near the bay was often in attendance, presumably feeding upon fish attracted to the garbage. This school's movements and direction could be predicted roughly in and out of the harbor by the schedule of the garbage barge though the porpoises and the barge did not normally travel together.

A similar habitual pattern was observed in relation to the shrimp trawling industry of the northern Gulf of California, Mexico. In this case otter trawls were dragged at slow speed across the sea bottom for a number of hours, usually with no dolphins in attendance. However, once the winch began to retrieve the net, dolphins were usually noted rapidly converging upon the vessel, often leaping free of the water enroute. As they arrived at the vessel they began to mill around her close aboard, as the catch was sorted on the afterdeck. When trash fish and invertebrates were shovelled overboard the dolphins picked off and ate individual prey items. They were often so close aboard that they could be touched with oars (Norris and Prescott, 1961). Similar behavior in relation to trawling vessels has been noted by Kleinenberg (1958) for *Tursiops truncatus*, and by Leatherwood (1975). In the latter case, groups of *Tursiops* were observed to follow trawls, presumably to feed on organisms stirred up by the net.

Habituation and play are probably both involved in such famous dolphin-human interactions as the Opononi indicents (see

Alpers, 1961), in which a large bottlenose dolphin swam with bathers and allowed swimmers to grasp its fin and flippers and take rides on its back. The behavior lasted for several months before the animal was found dead in a tidal pool. Saayman and Tayler (1971) described a similar incident at Fish Hoek Bay, Cape region of South Africa, in which two cow bottlenose dolphins established contact with bathers and allowed swimmers to ride by holding fins, or straddling the animals' backs. The animals shied away at once if a swimmer brought along strange objects. This seems to indicate that the dolphins knew when extraneous objects were involved. A number of other examples of this general sort could be cited, including the original "boy and the dolphin" story by Pliny the Elder (see a reprint of Pliny, 1962). Usually these are difficult to interpret in terms of learning or motivation on the part of the cetaceans.

For instance, Fairholm (1856) describes South Pacific natives being assisted by dolphins in mullet fishing. He reports that the familiarity was so great that the individual animals were recognized and named. The dolphins came in, driving the fish before them, and when the fish were concentrated natives threw nets over the fish. In the melee dolphins and men gathered fish together. Only in the precise area of Amity Bay was this known to occur and it was reported to have happened as long as men could remember. Busnel's (1972) report is of a very similar circumstance along the African coast, and was described earlier in this paper.

Play seems inextricably linked to learning and its functions are to be found at least in part in the establishment of finely tuned patterns such as leaping, bow-riding, familial interaction patterns, etc. It is a prominent part of dolphin school behavior, as it is in the behavior of most higher mammals (Eible-Eibesfeldt, 1967), and in fact could only be fully expressed in the relative safety of the school. It is common to observe young animals repeatedly "practicing" aerial patterns such as spins, leaps, fin and head slaps. For example, such repeated leaps in young animals have been reported by Norris and Prescott (1961) for North Pacific striped dolphins. Caldwell and Fields (1959) report surf-riding in Atlantic bottlenose dolphins in which about 12 animals split off from a larger school and repeatedly cruised inshore to play in the surf, riding waves in and out. Similar behavior, including surf riding by young animals, has been observed near Puerto Peñasco, Baja California, Mexico for the Pacific bottlenose dolphin by the senior author. Gunter (1943) describes Atlantic bottlenose dolphins "playing" with food fish by throwing them repeatedly into the air, and similar observations, both in nature and in captivity, were reported for the Pacific bottlenose dolphin by Norris and Prescott (1961), though in the latter case the behavior seemed to be related to food preparation, rather than play. The field observation was made in Estero de Punta Banda, Mexico and was much like Gunter's. Detailed observations of the behavior in captivity were made by Brown and Norris (1956) and the behavior was attributed to the need to soften and break up large prey

before swallowing. It not only included tossing the fish in the air (which randomized the end of the fish grasped by the dolphins) but included rubbing the fish against the bottom so firmly that rather prominent furrows were left in the bottom gravel. Ultimately the heads of the 1 to 1.5 kilogram yellowtail (Seriola dorsalis) were broken free and their headless flaccid bodies were swallowed.

What was especially interesting for our discussion here was that this behavior was carried out with great dispatch by animals which had been taken as adults in the wild, while two captive-born animals who had never been forced to deal with large food objects before attempted to imitate the others and then spent considerable time beyond that required by the wild animals in manipulating the fish, ultimately without success. Another revealing feature was that obvious ownership of a given fish existed. No animal touched another's fish even though it drifted to the bottom and was left for several minutes. It is not unlikely therefore, that dolphins, like other higher mammals, must practice, even as adults, in order to perform various difficult finely-integrated feats that are part of their lives.

Protective Behavior

An important function of the school clearly is the protection of the individuals that make it up, as was described in the section on sensory integration. In fact, Williams (1964) regards schooling behavior in fishes as a form of cover seeking, and we suggest protection from predation as probably causal in the

formation of cetacean schools. Further, school shape and internal structure seem related to protective mechanisms, varying according to circumstances.

In spinner, bottlenose and other schools, sharks are important predators (Norris and Dohl, ms.), as is clearly evident from the prevalence of scarring from shark bite, including both large species capable of killing adult dolphins and the smaller *Isistius* that apparently bites circular chunks from the blubber coat of tropical and subtropical dolphins and whales. The killer whale (*Orcinus orca*) is also known to prey upon dolphins (Eschricht, 1862).

Dolphins in schools seem exquisitely aware of their surroundings and a typical reaction to strange objects in the environment is avoidance and a tightening of the school. The placement of dolphin mothers and young in the central school during stress seems to be such a case. Townsend (1914) was one of the first to record such avoidance when he noted that Atlantic bottlenose dolphins seined at Cape Hatteras, North Carolina, refused to cross seine ropes, and even though the net had not yet come ashore the catch was accordingly considered secure. Similar experiments were run by us in Hawaii in which entire spinner dolphin schools were encircled and held by a single line at the surface from which 20 m lines hung at 3 m intervals. Schools were held for nearly 4 hours inside such "nets" even though ample room existed for the dolphins to swim untouched into the open sea beneath or through the vertical lines (Norris and Dohl, ms.).

Sometimes the "sending of scout" to investigate the source of disturbance has been suggested though we do not believe such purposive behavior to be established (Caldwell and Caldwell, 1964; Evans and Dreher, 1962). It may be akin to commonly observed behavior of a few animals leaving a large school to run the bow of a passing ship, or simple curiosity on the part of a few school members. Whether or not such scouting behavior represents true division of labor within the school is wholly unclear, and whether animals are in any way "sent" on a scounting mission is also unknown, and we think, unlikely.

Aggregation may occur without the presence of strange objects in the environment. For example, Uda and Nasu (1956) report bunching of whale schools during hurricanes, though one cannot be sure that such weather conditions induce fear in the animals concerned. It may be, for instance, that the noises of breaking waves cause acoustic interference, requiring closer order. Or it may be that storm waves simply entrain dolphin schools in their moving water mass. In fact, we have watched a school of pilot whales "surfing" on the breakers of a very rough, gale-swept sea without any indication that conditions were disturbing for the animals.

The fresh water platanistid dolphin, Inia, seems to form only small schools (Layne, 1958), even though in the same river system the delphinid genus Sotalia forms typical, though modest sized, schools (Norris, Harvey, Burzell and Krishna Kartha, 1973). In the case of Platanista gangetica, single animals or pairs seem the rule, though larger but scattered groups are

sometimes found (Kasuya and Aminul Haque, 1972).

If one views the entire cetacean group from whales to the smallest dolphins some regularity is evident. The largest whales hardly school at all in the normal sense of the word. They are usually widely spaced, solitary, or found in small sexual groups. On the feeding grounds aggregations may occur but these may well be related to a mutually available mass of food rather than to social cohesion. River dolphins form small groups, or are solitary; coastal dolphin species form small to moderate sized schools, while pelagic forms may at times form huge schools of several thousand animals (the numbers of animals in such large schools cannot, as yet, be estimated with any accuracy).

The variation in school size is exactly what would be predicted if predation were the basis for the degree of schooling tendency (Williams, 1964; Hamilton, 1971). Large whales seem singularly free of predation as adults, except for the occasional depradations of killer whales (Andrews, 1931). River dolphins in the Amazon-Orinoco system may suffer some predation from large fish or crocodilians and in the Ganges-Indus-Brahmaputra schooling appears, from reports, to be somewhat less developed, and there predators would also seem all but absent, expecially in the upper river systems (see Pilleri, 1970; Kasuya and Aminul Haque, 1972).

Responses to Environmental Cycles

Repetitive behavior patterns are common features of dolphin schools. Some, such as the presence of reproductive seasons in many cetaceans, clearly may result in cyclic phenomena in their schools. Sexual and age groupings may come and go, and a variety of cyclic, apparently sexually related migrations take place. The physiologic needs of the animals, such as energy conservation, may also be determinative, as for example in the reproductive migrations of harbor porpoises from icy northern waters to somewhat warmer southern ones (Dudok van Heel, 1962). Thermal balance seems crucial to these small cetaceans (the smallest cetaceans in northern waters - 1.8 to 2.0 meters total length) and they bear enormously large young in proportion to adult size (Kanwisher and Sundness, 1966). The case with larger whales seems of a somewhat different sort. Their long migrations to polar feeding areas (Mackintosh, 1946) seem more complex and are likely to be involved with the presence of seasonal food in polar seas, and perhaps to very low winter air temperatures (which would have to be breathed by overwintering animals) in polar latitude

Aside from such annual patterns it is becoming increasingly evident, as more detailed natural history accumulates for wild cetaceans, that daily patterns may be highly structured. The daily fluctuations in vocalization of bottlenosed dolphin found by Powell (1966) are a case in point. Norris and Dohl (ms.) found, for the Hawaiian spinner dolphin, that similar schooling patterns were repeated over and over on a daily basis, and that after some experience the observer could predict the sequence.

They found that nighttime was devoted to feeding along the submerged island slope usually about 200-2000 meters depth, where the island pitched sharply into the abyssal sea. During this period the animals dove in widely spread formation. Once morning came the school tightened, assuming a rank formation and movement toward shore occurred, with much aerial behavior. This was terminated during a period in which defacation was widespread throughout the school, presumably occasioned by the digestion of the night's catches. Dolphins caught in the afternoon had empty stomachs. To what extent food is stored during the night in the esophageal stomach is unknown.

Then, once the school came near the shore it moved into one of a few specific coves or lagoons (usually the same places are occupied rather regularly even within a given cove or lagoon). The rest period followed, discussed in detail earlier, in which rank formation changed to discoidal shape, with animals tightly packed. During this period, the diving pattern changed dramatically from short, shallow dives with the animals staying mostly at the surface in the ranked school, to a pattern of deeper dives, with only brief periods for respiration being spend on the surface. Spinning and vocalization, except for desultory clicks, ceased and subgroup structure became obscure. The school became a reactive system much like a fish school. No school leaders could be discerned except within subgroups where dominance hierarchies exist. Once rest periods were complete, individual alertness and activity increased, spinning and vocalization became strongly evident, as did play and

and reproductive behavior. The school reassumed a rough rank or linear formation and began movement out to sea, toward the evening feeding grounds.

Such diurnal patterns have been alluded to in observations of captive animals. Saayman, Tayler and Bower (1973) report diurnal changes in captive Indian Ocean bottlenose dolphin schools involving school shapes, activity, signalling and aggression. Bateson (1965) reported shifts in the social structure of a bispecies school (Stenella longirostris and S. attenuata) in which partners were changed when shifting from rest to play periods.

Morrow (1948) and Hunter (1968) discussed the breakdown of fish schooling during darkness. They assumed, therefore, that schooling was maintained principally by vision. It may be, however, that in the absence of visually oriented predators tight schooling is not longer the optimum strategy. Since schools are presumably essential for daytime survival of fish, dispersed fish must be assured of reassembly in the morning. Thus fish schools must simply go into a dispersed phase in darkness while maintaining some degree of cohesion as Breder (1954) perceived. This represents a close parallel to the condition observed in S. longirostris, namely that since the school state represents an equilibrium condition between opposing sets of dispersive or aggregative forces, different degrees of aggregation or dispersion occur at different times of day, varying from the tight aggregation of rest to the highly dispersed aggregation of diving and feeding schools. The dolphins, however, maintain a

good long distance sensory system, echolocation, regardless of light level.

Discussion

When one compares the structures of fish and dolphin schools it is clear that there are important differences between them. Large pelagic fish schools, for the most part, seem to be without cohesive subschool units, while such units typically comprise dolphin schools. In fact, several kinds of subschool units can be discerned in dolphin schools. Even during rest periods in dolphin schools one can discern subschool units, though resting animals behave in a much more unified fashion than when wholly alert. In fact, resting dolphin schools are reminiscent of fish schools in terms of total movement patterns. At such times they tend to act as a group, in a fashion that suggests that the main determinants of movements are the integrated sensory inputs of many school members; just as in the case with daytime fish schools.

Both fish and dolphin schools maintain quite discrete boundaries to their schools; school density does not trail off, in either case, toward the school margins, but is an abrupt change. The differences one sees between fish and dolphin schools are in internal structure within the envelope of the school, such as spacing, segregation of various classes of animals, and of individualized or group movement. What might account for these differences?

The most obvious causal difference lies in the complicated sociality of dolphins, and its general simplicity in schooling fish, and in a broad sense this is certainly a phylogenetic difference. That is, the general pattern of difference seems derivative from the piscene level of neural organization on one hand, and the mammalian level on the other. Typically, schooling fish do not show such social features as family or play groups. While schooling fish often show courtship patterns, both courtship and spawning tend to be strongly potentiated by similar simultaneous activity of other fish throughout the school and spawning is typically compressed into a short space of time. On the other hand, courtship and mating patterns are widely spread during the year in many dolphin species, and for mysticetes in at least the California gray whale (see Sauer, 1963 and Norris _et al_., in press). One often cannot determine simply from watching the behavior of dolphin schools when true mating takes place because reproductive patterns are so widely used in other social contexts. However, the timing of births gives a clue. In tropical and warm temperate dolphins the birth period tends to be broadly modal, often spanning several months or even the entire year. Field observation usually reveals a mixture of growth stages of young in a single dolphin school. To be sure, the timing of births in the migratory whales seems to be much more precise, coinciding with the stay at the warm water end of long migrations (see, for example, Dawbin, 1966).

Another way of viewing these differences between fish and dolphin schools is to focus on the persistent and complex nature of parental care and familial bonds in dolphins and their absence or simplicity in schooling fishes. Tayler and Saayman (1972) point out that the complexities of dolphin social life bear many resemblances to those in packs of baboons.

Note also that neither fish nor dolphin schools have been shown to have true leaders for short term directional movements such as are used in avoidance of strange objects in the environment. In fact, such leadership would probably defeat the responsiveness of school guidance as mediated by sensory integration. It seems that whether it be in open air or water, the third dimension makes it profitable for social animals as divergent as crustaceans, fish, dolphins or birds to use the integrated sensory inputs of many individuals to determine immediate group movements. Where leadership exists, in the form of dominance, it results in social ordering within and between the subgroups of a school, but there seems no evidence that the school as a whole receives direction directly from this source.

Long school movements, such as those to seasonal feeding grounds are more difficult to interpet. Some, such as those related to human fishing activities, clearly involve learning by some or many school members. It is probably that many non-human oriented movements also involve learning. Migrating bird flocks, for example, utilize the learning of older flock members in migration (Perdeck, 1958). Such learning clearly

results in directed movement but how it is transformed into directional signals for the entire group by the experienced dolphins or other animals isn't so obvious. One suspects that the determination of flock or school direction in such cases becomes cultural, and that a large fraction of the group has learned a direction. When events dictate migration or movement the "consensus" arrived at by such subtleties as the average precision of orientation and the average persistence of movement toward a given direction works in much the same fashion as immediate sensory integration to guide the animal group. Both dominance hierarchy and school or flock cohesion many then further potentiate such unified movement. That is, once a large number of a group project common signals about the direction of movement, the factors which determine school or flock structure act to insure its unified application.

Whether the large scale movements of fish, such as the albacore schools that circle the entire North Pacific Ocean (Shomura and Otsu, 1956) involve learning in this way is unclear, but it is quite possible that they do not.

None of this discussion requires that dolphin schools maintain complete structural integrity through time. In fact, Norris and Dohl (ms) have found that spinner schools are very fluid with respect to numbers at different locations and times. Recognizable individuals and subgroups could be found in groups ranging from a few animals to hundreds of individuals. Feeding schools often represented the coalescence of a number of smaller resting schools. Schools found at certain locations were

regularly larger than those found in other areas even though individual dolphins moved back and forth between the two areas.

The levels of difference of expression of schooling tendency and resultant structure between different widely separated phylogenetic groups seems to us to be a fertile field of investigation, albeit difficult. Especially, we think, the dolphin school is worthy of investigation because of the complexity of dolphin behavior and the forms it may take in the context of the school.

What might be the bases for such putative levels of additional complexity in dolphin schools? Two features of dolphin behavior impress us as providing a possible substrate for school complexity. They are: (1) the capacity for complex learning, (2) the capacity to understand contingency patterns within which learning occurs, or deuterolearning (Ruesch and Bateson, 1951). To clarify, the experiment of Pryor, Haag and O'Reilly (1969) showed that a dolphin could grasp generalized rules; namely that for each reward the dolphin was required to produce a novel piece of behavior, or to invent behavior. The grasping of this general rule or contingency upon learning happened quickly and was further modified by additional similar contingencies.

Let us look at these two capabilities and see if it is possible to discern how they might affect school dynamics in dolphins. There is much evidence that dolphins learn many things about their environment and that these learned things may be

translated into school behavior. We have recounted much of this behavior earlier in the section on "Learning". Clearly the response of dolphin schools to trawlers is of this sort, and one suspects that the associations between seine fishermen on shore and porpoise schools involves some level of learning on the part of the animals, and its translation into school behavior. The bow riding of dolphins is another case (see Lang, 1966). Around the world, dolphins of several species come to ships to ride almost effortlessly in the pressure and flow field around the bow or along the waist. Ships have plied the seas only briefly, thinking in evolutionary time, and one must look to a natural antecedent for an explanation. It is probably found in dolphins riding the waves at the heads of swimming whales, which has occasionally been observed. The translation to ships must be based on repeated learning at various places in the world. One can recount other examples, but these will suffice. It seems apparent that dolphin learning does indeed provide a high level of individual behavioral flexibility in nature, and that this is translated into local variations of behavior that one might call culture.

The translation from individual learned patterns to school behavior may occur by imitation, a feature well known in dolphin behavior. For instance, dolphins often learn from each other in oceanarium shows (Pryor, 1973) and sometimes it seems probable that simple observation by the animal is enough for learning, without actual practice of the pattern involved. For instance, not all members of captive schools will be asked to perform

certain behavior patterns, but many may learn them to some degree. Such an example is given by Norris (1974) in which socially subordinate bottlenose dolphins were shipped from one oceanarium to another, and when established in their new home without dominant animals, they began to perform the old patterns of the former dominant animals. The expression of such capacity in wild schools seems imperfect. The refusal of dolphins to travel with a collecting vessel, which may involve learning, is a common observation. Whole schools of Hawaiian spinner dolphins (10-60 animals approximately) may refuse to come to certain ships that have harrassed them. But in much larger schools (200-500 individuals) such as those of the Hawaiian spotted dolphin collective wariness is less clearly evident. Such patterns do not always seem to penetrate entire schools, or at least the wary part of such schools is not able to transmit its fear to other parts of the school. Thus it is not clear in such cases whether the animals that learn fear are able to teach some or all of their fellows, or whether when the collecting vessel arrives their "instantaneous fear" transmit a warning to others in the school. In large schools such transmission may be imperfect and because such aggregations may be transitory groupings no school wide behavior pattern may be possible to establish.

Vocal imitation is well known in odontocetes, both experimentally (Lilly, 1968, for bottlenose dolphin), and naturally (Backus and Schevill, 1966, for the sperm whale). While there is no clear evidence how such capability might be used in nature, it will be interesting to see, as our knowledge of wild schools

grows, if local dialectual signals exist.

At any rate, when we attempt to construct a conceptualization of how dolphin schools may function, using information such as is presented in this paper, we must allow into our thinking the demonstrated ability of dolphins to generalize. Such an admission will allow us to pose new and important possibilities that may then be testable.

On a simpler plane, a great many aspects of cetacean schooling important to contemporary ideas about group behavior are either unknown, or poorly understood, and these too should be gathered. Especially needed are quantitative studies of aspects of schooling since most of what we now know is anecdotal. For example, if one attempts to apply the theoretical constructs related to spacing of mobile animals discussed by Brown and Orians Orians (1970), to cetaceans, many gaps are at once apparent. What, for example, might home ranges or territories mean in cetacean groupings? Do schools ever exclude one another? In other words, is there "group space"? How do cetacean schools react to predators, and vice-versa? Can patterns of intra-school aggression be shown to develop aspects of school structure? How is resource partitioning and utilization related to cetacean schools? These, and other similar questions remain without definitive answers.

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References

Allen, F. M. (1916). The whalebone whales of New England. Mem. Boston Soc. Nat. Hist. 8(2), 107-322.

Alpers, A. (1961). Dolphin, the myth and the mammal. Boston: Houghton Mifflin Co.

Andrews, R. C. (1931). Whale hunting with gun and camera. A naturalist's account of the modern shore-whaling industry, of whales and their habits and of hunting experiences in various parts of the world. New York: Appleton and Co.

Arsen'ev, V. A. (1939). Distributions and migrations of the beluga in the far east. Izvest. Tikhook. (TINRO), 1-108 [Russian].

Backus, R. H. and Schevill, W. E. (1966). Physeter clicks. In: Whales, Dolphins and Porpoises (Ed. by K. S. Norris), Ch. 22, Univer. Calif. Press.

Barabash-Nikiforov, I. C. (1940). Cetacean fauna of the Black Sea - Its origins and composition. Izd. Voronezhskogo Universiteta 12 (cited in Tomilin, 1967).

Bartholomew, G. A. (1942). The fishing activites of double-crested cormorants of San Francisco Bay. Condor, 44, 13-21.

Bateson, G. (1965). The cetacean community in Whaler's Cove - Sea Life Park. Excerpt from draft of Career Development Award (K3-NH-21, 931) National Institutes of Health. Mimeo.

Bateson, G. (1966). Problems in cetacean and other mammalian communication. In: Whales, Dolphins and Porpoises (Ed. by K. S. Norris). Univ. Calif. Press, Ch. 25.

Breder, C. M. Jr. (1954). Equations descriptive of fish schools and other animal aggregations. Ecology 35(3), 361-370.

Breder, C. M. Jr. (1965). Vortices and fish schools. Zoologica, 50(2), 97-114.

Breder, C. M. Jr. (1967). On the survival value of fish schools. Zoologica, 52(2), 25-40.

Brock, V. E. & Riffenburgh, R. H. (1960). Fish schooling: a possible factor in reducing predation. J. Cons. Perm. Int. Explor. Mer., 25(3), 307-317.

Brown, D. H., Caldwell, D. K. & Caldwell, M. C. (1966). Observations on the behavior of wild and captive false killer whales with notes on associated behavior of other general of captive delphinids. Los Angeles County Mus. Nat. Hist. Contrib. Sci., 95, 1-32.

Brown, D. H. & Norris, K. S. (1956). Observations of captive and wild cetaceans. Jour. Mammalogy, 37(3), 311-326.

Brown, J. L. & Orians, G. H. (1970). Spacing patterns in mobile animals. Ann. Rev. Ecol. and Syst., vol. I, 239-262.

Brown, S. G. (1954). The movements of fin and blue whales in Antarctic waters. Norsk-Hvalfangst-Tidende, 43(6), 301-309.

Busnel, R. G. (1972). Symbiotic relationship between man and dolphins. Trans. N.Y. Acad. Sci., Ser. 11, 35(2), 112-131.

Caldwell, D. K. & Fields, H. M. (1959). Surf-riding by Atlantic bottle-nosed dolphins. J. Mamm., 40(3), 454-455.

Caldwell, M. C. & Caldwell, D. K. (1964). Experimental studies of factors involved in care-giving behavior in three species of the cetacean family Delphinidae. Bull. So. Calif. Acad. Sci., 63(1), 1-20.

Caldwell, M. C., & Caldwell, D. K. (1966). Epimeletic (care-giving) behavior in cetacea. In: Whales, Dolphins and Porpoises (Ed. by K. S. Norris). Ch. 33, Univ. of Calif. Press.

Caldwell, D. K., Caldwell, M. C., & Rice, D. W. (1966) Behavior of the sperm whale Physeter catodon L. In: Whales, Dolphins and Porpoises (Ed. by K. S. Norris). Ch. 30, Univ. Calif. Press.

Caldwell, M. C. & Caldwell, D. K. (1967). Intraspecific transfer of information via the pulsed sound in captive cetaceans. In: Animal Sonar Systems, Biology and Bionics, Vol. II. (Ed. by R. G. Busnel). Frascati, Italy: N.A.T.O. Advanced Study Inst., Frascati Symp.

Caldwell, M. C. & Caldwell, D. K. (1967). Dolphin community Life. Los Angeles County Mus. Quarterly, 5(4), 12-15.

Caldwell, M. C. & Caldwell, D. K. (1972). Behavior of marine mammals. In: Mammals of the Sea. Biology and Medicine. (Ed. by S. H. Ridgway). Ch. 6, Springfield, Ill: C. Thomas.

Caldwell, D. K. & Caldwell, M. C. (1972). Senses and communications. In: Mammals of the Sea. Biology and Medicine. (Ed. by S. H. Ridgway). Ch. 7, Springfield, Ill: C. Thomas.

Chapskii, K. K. (1941). Marine mammals of the Soviet Arctic. Izdat. Glavsev Leningrad-Moscow [Russian - cited in Tomilin, 1967].

Clarke, R. (1957). Migrations of marine mammals. Norsk-Hvalfangst-Tidende, 46(11), 609-630.

Cody, M. L. (1971). Finch flocks in the Mohave Desert. Theoretical Population Biol., 2(2), 142-158.

Cummings, W. C. & Thompson, P. O. (1971). Gray whales, *Eschrichtius robustus*, avoid the underwater sounds of killer whales, *Orcinus orca*. Fishery Bulletin, 69(3), 525-530.

Cummings, W. C., Fish, J. F. & Thompson, P. O. (1972). Sound production and other behavior of southern right whales, *Eubalaena glacialis.* Trans. San Diego Soc. Nat. Hist., 17(1), 1-14.

Dakin, W. J. (1934). Whalemen adventurers, the story of whaling in Australian waters and other southern seas related thereto, from the days of sails to modern times. Sydney: Angus & Robertson, Ltd.

Dawbin, W. H. (1966). The seasonal migratory cycle of humpback whales. In: Whales, Dolphins and Porpoises (Ed. by K. S. Norris). Ch. 9, Univ. Calif. Press.

Dohl, T. P., Norris, K. S. & Kang, I. (1974). A porpoise hybrid *Tursiops* x *Steno*. Jour. Mammal., 55(1), 217-221.

Dreher, J. (1966). Cetacean communication: small group experiment. In: Whales, Dolphins and Porpoises (Ed. by K. S. Norris) Ch. 23, Univ. Calif. Press.

Dudok van Heel, W. H. (1962). Sound and cetacea. Netherlands Jour. Sea Res., 1, 407-507.

Eberhardt, R. L. & Norris, K. S. (1964). Observations of newborn Pacific gray whales on Mexican calving grounds. Jour. Mammal., 45(1), 88-95.

Eibl-Eibesfeldt, I. (1967). Concepts of ethology and their significance in the study of human behavior. From: Early Behavior: Comparative and Development Approaches (Ed. by H. W. Stevenson). John Wiley & Sons.

Eschricht, D. F. (1866). On the species of the genus *Orca* inhabiting the northern seas. Recent Mem. on the Cetacea (Ed. by W. H. Flower).

Evans, W. E. (1971). Orientation behavior of delphinids: radio telemetric studies. Ann. New York Acad. Sci., 188, 142-160.

Evans, W. E. & Dreher, J. J. (1962). Observations on scouting behavior and associated sound productions by the Pacific bottlenose porpoise (*Tursiops gilli* Dall). Bull. So. Calif. Acad. Sci., 61(4), 217-226.

Evans, W. E. & Bastian, J. (1969). Marine mammal communications: Social and ecological factors. In: The Biology of Marine Mammals (Ed. by H. T. Andersen). Ch. 11, New York: Academic Press.

Evans, W. E. (1974). Radio telemetric studies of two species of small odontocete cetaceans: preliminary results. In: The Whale Problem (Ed. by W. E. Schevill; C. Ray and K. S. Norris, Consulting Eds.). Ch. 18, Harvard Univ. Press.

Evans, W. E. & Dreher, J. J. (1962). Observations on scouting behavior and associated sound production by the Pacific bottlenose porpoise (Tursiops gilli Dall). Bull. So. Calif. Acad. Sci., 61(4), 217-226.

Evans, W. E. (1975). The biology of the common dolphin, Delphinus delphis Linnaeus. Doctoral Dissertation, Univ. of Calif., Los Angeles.

Fairholme, __ (1856). The blacks of Moreton Bay and the porpoises. Proc. Zool.Soc. London, 24, 353-354.

Fink, B. D. (1959). Observations of porpoise predation on a school of Pacific sardines. Calif. Fish and Game, 45(3), 216-217.

Fish, J. F. & Vania, J. S. (1971). Killer whale, Orcinus orca, sounds repel white whales, Delphinapterus leucas. Fishery Bulletin, 69, 531-535.

Fitch, J. E. & Brownell, R. L.,Jr. (1968). Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Bd. Canada, 25(12), 2561-2574.

Geptner, V. G. (1930). Material for a study of the geographic distribution and life history of the Beluga. Trudy Inst. Zool. Moscow Univ., 4(2), 1-110 [Russian].

Gilmore, R. M. (1961). The Story of the Gray Whale, 2nd Ed. San Diego: privately printed.

Golenchenko, P. (1949). Cited in Mammals of the U.S.S.R. and Adjacent Countries, Vol. IX. Cetaceans. (Ed. by A. G. Tomilin). Trans. from Izdatel'stuo Akademi Nauk SSSR Moskua 1957, p. 488. Translated Israel Proj. Scient. Trans. Jerusalem, 1967, xxi + 717 p.

Gray, R. (1887). Notes on a voyage to Greenland seas in 1886. Zoologist, XI, 122-124.

Green, R. E., Perrin, W. R. & Petrich, B. P. The American Tuna Purse Seine Fishery. Modern Fishing Gear of the World. 3, 182-194. London: Fishing News (Books), Ltd.

Gunter, G. (1943). Contributions to the natural history of the bottlenose dolphin Tursiops truncatus (Montagu) on the Texas coast, with particular reference to food habits. J. Mamm., 23(3), 267-275.

Gunter, G. (1954). Mammals of the Gulf of Mexico. U. S. Fish and Wildlife Service, Fishery Bull., 55, 543-551.

Hamilton, W. D. (1971). Geometry for the selfish herd. Jour. Theor. Biol. 31, 295-311.

Hamilton, W. J. & Watt, K. E. F. (1970). Refuging. Paper 4010, Ann. Rev. Ecology and Systematics, vol. 1, 263-286.

Hart, T. J. (1935). On the diatoms of the skin films of whales and their possible bearing on the problems of whale movements. Disc. Rept. 10, 247-282.

Herman, L. M. & Arbeit, W. R. (1973). Stimulus control and auditory discrimination learning sets in the bottlenose dolphin. J. Exp. Anal. Behav., 19, 379-394.

Hester, F. J., Hunter, J. R. & Whitney, R. R. (1963). Jumping and spinning behavior in the spinning porpoise. J. Mamm., 44(4), 586-588.

Hubbs, D. L.(1953). Dolphins protecting dead young. J. Mamm., 34(4), 498.

Hunter, J. (1968). Effect of light on schooling and feeding of jack mackerel Trachurus symmetricus. J. Fish. Res. Bd. Canada, 25(2), 393-407.

Kanwisher, J. & Sundnes, G. (1966). Thermal regulation in cetaceans. In: Whales, Dolphins and Porpoises (Ed. by K. S. Norris). Ch. 18, Univ. Calif. Press.

Kasuya, T. & Aminul Haque, A. K. M. (1972). Some information on distribution and seasonal movement of the Ganges dolphin. Sci. Repts. Whales Res. Inst., 24, 109-115.

Kellogg, R. (1929). What is known of the migrations of some of the whalebone whales. Ann. Rept. Smithsonian Inst. for 1928, 467-494.

Kellogg, W. N. & Rice, C. E. (1966). Visual discrimination and problem solving in a bottlenose porpoise. In: Whales, Dolphins and Porpoises. (Ed. by K. S. Norris). Ch. 32, Univ. Calif. Press.

Kleinenberg, S. E. (1938). Quelques donneas sur l'alimentation de Tursiops tursio. Fabr. dans la mer noire Bull. Soc. Nat. Muscov 47, 406-413.

Krebs, J. R. (1974). Colonial nesting and social feeding as strategies for exploiting food resources in the great Blue Heron (Ardea herodias), Behaviour LI 1-2, 99-134.

Kruuk, H. (1972). The Spotted Hyena. Chicago Univ. Press.

Lang, T. G. (1966). Hydrodynamic analysis of cetacean performance. In Whales, Dolphins and Porpoises. (Ed. by K. S. Norris). Ch. 19, Univ. Calif. Press.

Layne, J. N. (1958). Observations on freshwater dolphins in the upper Amazon. J. Mamm., 39, 1-22.

Layne, J. N. & Caldwell, D. K. (1964). Behavior of the Amazon dolphin, Inia geoffrensis (Blainville) in captivity. Zoologica, 49, 81-108.

Leatherwood, J. S. (1975). Some observations of feeding behavior of bottlenosed (Tursiops truncatus) in the northern Gulf of Mexico and (Tursiops cf. T. gilli) off southern California, Baja California, and Nayarit, Mexico. Marine Fish. Rev. 37(9), 10-16.

Leatherwood, J. S. & Samaris, W. F. (1974). Some observations of killer whales, Orcinus orca, attacking other marine mammals. Proc. So. Calif. Acad. Science Meeting, Fullerton, CA.

Lewontin, R. C. (1970). The units of selection. Ann. Rev. Ecol. and System., 1-18.

Lilly, J. C. (1963). Distress call of the bottlenose dolphin: stimuli and evoked behavioral responses. Science, 139, 116-118.

Lilly, J. C., Miller, A. M. & Truby, H. M. (1968) Reprogramming of the sonic output of the dolphin: sonic burst count matching. Jour. Acoust. Soc. Amer., 43(6), 1412-1424.

MacAskie, I. V. (1966). Unusual example of group behavior by killer whales (Orcinus rectipinna). Murrelet, 47(2), 38.

Macintosh, N. (1946). The natural history of whalebone whales. Biol. Rev., 21, 60-74.

Major, P. (1976). The behavioral ecology of predator-prey interactions in schooling fish. Ph.D. Dissertation, Univ. California, Santa Cruz.

Mal'm, E. N. (1946). Dolphins of the Black Sea. Izdatel'stvo Akademii Nauk SSSR Leningrad, 1-23 (cited in Tomilin, 1967).

Matthews, L. H. (1954). The migration of mammals. Discovery, 15, 202-206.

McBride, A. (1940). Meet Mister Porpoise. Natural History Magazine 45:16-29.

McBride, A. F. & Hebb, D. O. (1948). Behavior of the captive bottlenose dolphin, Tursiops truncatus. J. Comp. & Physiol. Psych. 41(2), 111-123.

McBride, A. F. & Kritzler, H. (1951). Observations on pregnancy, parturition and post-natal behavior in the bottlenose dolphin. J. Mamm., 32(3), 251-266.

McFarland, W. N. & Moss, S. A. (1967). Internal behavior of fish schools. Science, 156(3772), 260-262.

Mitchell, E. (1965). Evidence for mass stranding of the false killer whale (Pseudorca crassidens) in the eastern North Pacific Ocean. Norsk-Hvalfangst-Tidende, 8, 172-177.

Møhl-Hansen, M. (1954). Investigation on reproduction and growth of the porpoise from the Baltic. Vidensk. Medd. Dansk. Naturh. Fores., 116, 369-396.

Morrow, J. E. Jr. (1948). Schooling behavior in fishes. Rev. Biol., 23(1), 27-38.

Neave, D. J. & Wright, B. S. (1968). Seasonal migrations of the harbor porpoise (Phocoena phocoena) and other cetacea in the Bay of Fundy. J. Mamm., 49(2), 259-264.

Newman, M. A. (1968). Narwhals: Sea going unicorns of the north Pacific. Search, 17-18.

Nielsen, N. & Degerbøhl (1930). Biologiske iagttagelser over og mallinger af huidvalen og dues fostre. Saertryk af Meddelelser om Gronland, 77: Copenhagen (cited in Tomilin, 1967).

Nishiwaki, M. (1962). Aerial photographs show sperm whales' interesting habits. Norst Hvalfangstid., 51, 395-398.

Norris, K. S. (1965). Trained porpoise released in the open sea. Science, 147, 1048-1050.

Norris, K. S. (1967). Some observations on the migration and orientation of marine mammals. In: Animal Orientation and Navigation. Proc. 27th Ann. Biol. Coll. Oregon State Univ., Corvallis, Oregon. pp. 101-125.

Norris, K. S. (1967). Aggressive behavior in cetacea. In: Aggression and Defense: Natural Mechanisms and Social Patterns. (Ed. by C. D. Clemente and D. B. Lindsley). Proc. 5th Conf. Brain Function. Berkeley, Univ. Calif. Press.

Norris, K. S., Ed. (1966). Whales, Dolphins and Porpoises. Berkeley and Los Angeles, Univ. Calif. Press. XV + 789 p.

Norris, K. S. (1974). The Porpoise Watcher. New York, Norton & Norton Press. 250 p.

Norris, K. S. & Prescott, J. H. (1961). Observation on Pacific cetaceans of Californian and Mexican waters. Univ. Calif. Publ. Zool., 63, 291-402.

Norris, K. S., Harvey, G. W., Burzell, L. A. & Krishna Kartha, T. D. (1972). Sound production in the freshwater porpoise Sotalia cf. fluviatilis Gervais and Deville and Inia geoffrensis Blainville in the Rio Nego, Brazil. Investigations on Cetaceans, vol. IV, 251-260.

Norris, K. S. & Gentry, R. L. (1974). Capture and harnessing of young California gray whales, Eschrichtius robustus. Marine Fish. Rev., 36(4), 58-64.

Norris, K. S., Goodman, R., Villa-Ramirez, B. & Hobbs, L. (in press). The behavior of California gray whales (Eschrichtius robustus) in southern Baja California, Mexico. Fisheries Bull.

Norris, K. S. & Dohl, T. P. (ms.) The behavior of the Hawaiian spinner porpoise, Stenella longirostris.

Ohsumi, S. (1971). Some investigations on the school structure of sperm whales. Sci. Repts. Whales Research Institute, 23, 1-25.

Payne, R. & Webb, D. (1971). Orientation by means of long range acoustic signalling in baleen whales. Ann. New York Acad. Sci., 188, 110-141.

Perdeck, A. C. (1958). Two types of orientation in migrating starlings Sturnus vulgaris L. and Chaffinches Fringilla coelebs L., as revealed by displacement experiments. Ardea 46, 1-37.

Perrin, W. F. (1970). Color pattern of the eastern Pacific spotted porpoise Stenella graffmanni Lonnberg (Cetacean Delphinidae). Zoologica, 54, 135-142.

Perrin, W. F. (1972a). Variation and taxonomy of spotted and spinner porpoises (genus Stenella) of the eastern tropical Pacific and Hawaii. Ph.D. dissertation, Univ. Calif. Los Angeles, Zoology, XXVL + 490 p.

Perrin, W. F. (1972b). Color patterns of spinner porpoises (Stenella cf. S. longirostris) of the Eastern Pacific and Hawaii, with comments on delphinid pigmentation. Fisheries Bull., 70(3), 983-1003.

Pike, G. (1962). Migration and feeding of the gray whale (Eschrichtius gibbosus). J. Fish. Res. Bd. Canada, 19, 815-838.

Pilleri, G. (1970). Observations on the behavior of Platanista gangetica in the Indus and Brahmaputra Rivers. In: Investigations on Cetacea. (Ed. by G. Pilleri). Benteli Ag, Berne-Bumpliz, Switzerland.

Pilleri, G. & Knuckey, J. (1967). The distribution, navigation and orientation by the sun of Delphinus delphis L. in the western Mediterranean. Experientia, 24(4), 394-396.

Pliny the Elder (1962). In: Natural History (Ed. by P. Turner), 9th Book; Mermaids and Mermen. Centaur Press.

Powell, B. A. (1966). Periodicity of vocal activity of captive Atlantic bottlenose dolphins: Tursiops truncatus. Bull. So. Calif. Acad. Sci., 64(4), 237-244.

Pryor, K. W., Haag, R. & O'Reilly, J. (1969). The creative porpoise: training for novel behavior. Jour. Exp. Anal. Behavior, 12, 653-661.

Pryor, K. S. (1973). Behavior and learning in porpoises and whales. Naturwissenshaften, 60, 412-420.

Radakov, D. V. (1967). The biological and practical importance of schooling behavior in fishes. Proc. FAO Conf. on Fish Behavior in Relation to Fishing Techniques and Tactics, Bergen, Norway.

Rae, B. B. (1965). The food of the common porpoise (Phocoena phocoena). J. Zool., 146, 114-122.

Raynor, G. W. (1940). Whale markings: Progress and Results Dec. 1939. Disc. Repts. XIX, 245-284, and 1948, Whale marking II, Distribution of Blue, Fin and Humpback whales marked from 1932 to 1938. Disc. Repts. XXV, 31-38.

Ruesch, J. & Bateson, G. (1951). Communication: the social matrix of psychiatry. New York: Norton and Norton.

Saayman, G. S. & Tayler, C. K. (1971). Responses to man of captive and free-ranging cetaceans. Baralogia; Proc. 1st and 2nd So. African Symposium for Underwater Sciences. University Pretoria 1-9.

Saayman, G. S., Tayler, C. K. and Bower, D. (1973). Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (Tursiops aduncus Ehrenburg). Behavior, XLIV (3-4), 212-233.

Saayman, G. S., Bowér, D. & Tayler, C. K. (1972). Observations on inshore and pelagic dolphins on the southeastern Cape coast of South Africa. Koedoe, 15, 1-24.

Sauer, E. G. F. (1963). Courtship and copulation of the gray whale in the Bering Sea at St. Lawrence Island, Alaska. Psychol. Forsch. 27, 157-174.

Schaller, G. (1972). The Serengeti Lion. Chicago Univ. Press.

Scheffer, V. B. (1949). The Dall porpoise, Phocoenoides dalli, in Alaska. J. Mamm., 30(2), 116-121.

Scheffer, V. B. (1950). The striped dolphin, Lagenorhynchus obliquidens Gill, 1865, on the coast of North America. Amer. Midl. Nat., 44, 750-758.

Sergeant, D. E. (1959). On the evolution of life histories in the Delphinidae. Sect. 3., Sept. 1959, Population of the Sea. The Role of Ethology in Oceanography.

Sergeant, D. E. (1962). The biology of the pilot or pothead whale Globicephala melaena (Traill) in Newfoundland waters. Bull. Fish. Res. Bd. Canada, 132, 84 p.

Shallenberger, R. J. (1973). Breeding biology, homing behavior, and communication patterns of the wedge-tailed shearwater Puffinus pacificus chlororhynchus. Ph.D. dissertation, University of California, Los Angeles, 438 p.

Shaw, E. (1970). Schooling in fishes: critique and review. In: Development and Evolution of Behavior (L. Arenson et al., editors). W. H. Freeman and Co., San Francisco.

Shomura, R. S., and T. Otsu. (1956). Central North Pacific albacore surveys, January 1954-February 1955. U. S. Fish and Wildlife Surv. Special Sci. Report, Fisheries, 173; 1-29.

Siebenaler, J. B. & Caldwell, D. K. (1956). Cooperation among adult dolphins. J. Mamm., 37(1), 126-128.

Slijper, E. J. & van Utrecht, W. L. (1959). Observing whales. Norsk Hvalfangst-Tidende, 3, 101-117.

Tarasevich, M. N. (1957). Comparison of the composition of herds of aquatic and amphibious mammals [Russian]. VNIRO, 33, 199-218.

Tavolga, M. C. (1966). Behavior of the bottlenose dolphin (Tursiops truncatus): Social interactions in a captive colony. In: Whales, Dolphins and Porpoises (Ed. by K. S. Norris), Ch. 31, Univ. Calif. Press.

Tavolga, M. C. & Essapian, F. S. (1957). The behavior of the bottlenosed dolphin (Tursiops truncatus): mating, pregnancy, parturition, and mother-infant behavior. Zoologica, 42, 11-31.

Tayler, C. K. & Saaymen, G. S. (1972). The social organization and behavior of dolphins (Tursiops aduncus) and baboons (Papio ursinus): Some comparisons and assessments. Ann. Cape Rov. Mus. Nat. His., 9, 11-49.

Tayler, C. K. & Saayman, G. S. (1973). Imitative behavior by Indian Ocean bottlenose dolphins (Tursiops aduncus) in captivity. Behavior, 19(3-4), 286-298.

Tomilin, A. G. (1960). O migratsuakh, geograficheskikh rasakh, termorefuliatsii i vliianii termperatury sredy na rasprostraneni kitoobraznykh. In: Migratsii Zhivotnykh, No. 2 Akademua Nauk SSSR, 3-26.

Tomilin, A. G. (1967). Mammals of the U.S.S.R. and adjacent countries. Vol. IX Cetacea. Izdatel'stvo Akademii Nauk SSSR Moskva 1957. Translated Israel Prog. Scient. Trans. Jerusalem 1967. xxi + 717 p.

Townsend, C. H. (1914). The porpoise in captivity. Zoologica 1(16), 288-299.

True, F. W. (1885). The bottle-nose dolphin Tursiops tursio as seen at Cape May, New Jersey. Science, 5(116), 336-339.

True, F. W. (1890). Observations on the life history of the bottlenose porpoise. Proc. USNM, 13, 195-203.

Tsalkin, V. I. (138). Respredelinie obyknovennogo chemomorskogo del'fina (D. delphis) letne-osennii period. Trudy Azova-Chernomomorskogo Nauchno-Issledovatel'skogo Instituta Rybnuga Khozyaistva No. 2 (cited in Tomilin, 1967).

Uda, M. & Nasu, K. (1956). Studies of the whaling grounds in the northern sea region of the Pacific Ocean in relation to the meteorological and oceanographic conditions (Pt. 1). Sci. Rept. Whales Res. Inst., 11, 163-179.

Watkins, W. A. & Schevill, W. E. (1972). Sound source location by arrival times on a non-rigid three-dimensional hydroplane array. Deep-Sea Res., 19, 691-706.

Wilke, F., Taniwaki, T. & Kuroda, N. (1953). Phocoenoides and Lagenorhynchus in Japan, with notes on hunting. J. Mamm. 34(4), 488-497.

Williams, G. C. (1964). Measurements of consociation among fishes and comments on the evolution of schooling. Pubs. Mich. State Univ. Mus., 2, 351-383.

Zahavi, A. (1971). The function of pre-roost gatherings and communal roosts. The Ibid, 113(1), 106-109.

Zenkovich, B. A. (1973). Vokrug sucta za Kitami (Around the world after whales). Cited in Tomilin, A. G., 1967, Mammals in the U.S.S.R. and Adjacent Countries, vol. IX Cetacea, Trans. Israel, Prog. P. 333, Scientific Trans. Jerusalem, xxix, 717 p.

Figure Captions

Figure 1. Association of feeding common dolphin schools (<u>Delphinus delphis</u>) with subsurface topography in the southern California bight area. Note that most sightings are over escarpments and sea mounts, with relatively fewer sightings in the intervening areas of low bottom relief. From Evans, 1971.

Figure 2. The duration of feeding and courtship activities of bottlenose dolphins (<u>Tursiops</u>) in Plettenberg Bay, South Africa, in relation to time of day. From Saayman, Tayler and Bower, 1973.

Figure 3. Echelon swimming, or assisted locomotion, between a roughtooth dolphin mother (<u>Steno bredanensis</u>) and her hybrid baby (<u>Steno</u> x <u>Tursiops truncatus</u>) shortly after birth. Note the contact of the baby's inboard pectoral fin with the mother's side and the cupped flaccid flukes extended directly to the rear. In this position the young is "dragged" along without locomotory movements of its own as the mother swims.

Figure 4. A comparison of day length regimes of migrating California gray whales and Southern Hemisphere humpback whales. Gray whale data mostly from Pike, 1962. Humpback whale data from Dawbin, 1966.

Figure 5. Scarring of a female Cuvier's Beaked Whale (Ziphius cavirostris). The separation and depth of the scars suggest that they were made by an adult male of the same species. Specimen found stranded on February 21, 1956, Pebbly Beach, Santa Catalina Island, California.

Figure 6. Nursing posture between roughtooth dolphin mother (Steno bredanensis) and her hybrid baby (Steno x Tursiops truncatus).

Figure 7. Epimeletic behavior in a mother-young dolphin pair. A stillborn baby is carried on the snout of its mother, sometimes until decomposition is far advanced (see text).

Figure 8. A stranded school of Pacific pilot whales (Globicephala sp.) at 4.8 km N. La Paz, Baja California, Mexico, on May 12, 1959.

Figure 9. Mean levels of vocal activity in relation to time of day for five Atlantic bottlenose dolphins (Tursiops truncatus). From Powell, 1967.

Figure 10. A mixed captive school of spinner dolphins (*Stenella longirostris*) and spotted dolphins (*Stenella attenuata*) at Sea Life Park, Hawaii. Note the black beak tips of spinner dolphins above, and the white beak tips of spotted dolphins below. These may be species specific school identification marks to animals at sea. Note also the pectoral contact between the animals.

Figure 11. Systems of ascendancy of threat and beak-genital propulsion in a captive mixed spotted dolphin (*Stenella attenuata*)-spinner dolphin (*Stenella longirostris*) school, at Sea Life Park, Hawaii (see Bateson, 1965). Kahili - *S. attenuata* male, Lei - *S. attenuata* female, Moki - *S. longirostris* male, Akamai - *S. longirostris* male, Haole - *S. longirostris* male, Mamo - *S. longirostris* female, Limu - *S. longirostris* male.

Figure 12. Beak-genital propulsion in captive spinner dolphins at the Oceanic Institute, Oahu, Hawaii. Male above; female below.

Figure 13. Frame-by-frame composite of a spinning sequence in a young male eastern tropical Pacific spinner dolphin, *Stenella longirostris*. From Hester, Hunter and Whitney, 1963.

Figure 14. Ventral pattern of the tonina, Cephalorhynchus eutropia, at Corrál , Chile. Note sharp demarcation of ventral and lateral patterns, dark marking on genital area and white mark in axilla.

Figure 15. Deuterolearning in the roughtooth dolphin, Steno bredanensis. The porpoise was rewarded for novel behavior only, in this session, but started with two previously learned behavior patterns; the tailslap and the sideswipe. Then, after 2.5 minutes a wholly novel behavior, an inverted leap or "backflip" was offered and rewarded, and was then presented to the exclusion of other behavior. From Pryor, Haag and O'Reilly, 1969.